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Maximum in the minimum: Biogeography of land snails from the Ningbing Ranges and Jeremiah Hills, northeast Kimberley, Western Australia

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ABSTRACT

The Ningbing Ranges and Jeremiah Hills are home to what is perhaps the greatest concentration of short range restricted endemic species found anywhere in the world. A radiation of more than 28 mainly allopatric species of camaenid land snails is packed into 52 km of limestone hills. The median linear range of a species is 1.65 km; the median area range is 0.825 km^2. Located in the far northeastern tip of Western Australia between the east bank of the Ord River and the Northern Territory border, the Ningbing Ranges and Jeremiah Hills are Devonian limestone reef remnants, generally much less than 500 meters wide, that rarely reach 50-60 meters in height. The Ningbing Ranges have a length of 43.5 km; the Jeremiah Hills occupy a triangular area some 8.4 km on a side.

Most of this remarkable diversity occurs within three restricted endemic genera of the pulmonate land snail family Camaenidae — *Ningbingia* Solem, 1981 with six species and one subspecies; *Turgenitubulus* Solem, 1981 with eight species; and *Cristilabrum* Solem, 1981 with eleven described and another probably new species. It is anticipated that additional species will be discovered. Another restricted endemic, short range species of the East Kimberley genus, *Ordtrachia* Solem, 1984 is known from a small eastern outlier of the Jeremiah Hills (*O. elegans* Solem, 1988). This is an *in situ*, still exuberant, radiation filling all habitable parts of the area, not an example of constricted ranges in a group approaching extinction.

In addition to the above endemics that occupy only a portion of the ranges, two land snail taxa, a hydrocenid prosobranch, *Georissa*, new species and a pupillid, *Gyliotrachela ningbingia* Solem, 1981, are common throughout much of the area. The nearest recorded species of *Georissa* Blanford, 1864 are in Indonesia and coastal Queensland. The other Australian species of *Gyliotrachela* live in the Napier Range of the southwest Kimberley, near Katherine, Northern Territory, and the Chillagoe Caves area of northern Queensland (Solem, 1981c).

The above 30 species of endemic and restricted land snails are supplemented by a number of much more widely distributed, but also indigenous taxa: 1) eight species that occur within the main masses of at least the Ningbing Ranges (*Gastrocopta*, new species, *Pupoides pacificus* [Pfeiffer, 1846], *Eremopeas interioris* [Tate, 1894], *Stenopylis coarctata* [Moellendorff, 1894], *Discocharopa aperta* [Moellendorff, 1888], *Austrosuccinea* sp., *Westracystis lissus* [E. A. Smith, 1894], and Xanthomelon obliquirugosa [E. A. Smith, 1894]); 2) one camaenid, *Torresitrachia weaberana* Solem, 1979, that lives on the dry fringes of the area; 3) one species, *Pupisoma orcula* (Benson, 1850), recorded once from the Central Ningbing Range; and 4) three species (*Pupisoma* sp., *Nesopupa mooreana* [E. A. Smith, 1894], and *Coneuplecta microconus* [Mousson, 1865]) that have been found only in the wet margins of Brolga Spring or seasonally wet margins of the North Ningbing Range.

The total known land snail fauna is thus 43 species. A number of additional species found in nearby non-limestone hill systems help to define the fauna of the limestone ranges.

The climate of the Ningbing region is monsoonal, with an average rainfall of about 776 mm, nearly all between early November and mid-April of the next year. Snail activity nights (SAN) probably average about 78/year, with the rest spent in partial to deep aestivation. The Ningbing-Jeremiah Hills area is much drier than the Mitchell Plateau to the west or Darwin region to the east. The latter have rain forest patches and nearly closed canopy forest, while the Ningbings have open savannah type cover with baobabs the most conspicuous tree.

The restricted and short range endemic camaenid genera are allopatric, with *Ningbingia* in the North Ningbing Range; *Turgenitubulus* in the Central Ningbing Range, The Gorge, and The Pillars; *Cristilabrum* in a small portion of the Central Ningbing Range (but never sympatric with *Turgenitubulus*), South Ningbing Range, and Jeremiah Hills. All species in these genera live only within rubble or crevices on the limestone outcrops. None have been found living in plains areas or on neighbouring sandstone hills. The ranges of all species are continuous, never interrupted by an intrusive zone of another species. Four species (Table 6) have ranges broken up by uninhabitable stretches of mud or alluvial plains, so that their linear ranges are longer than their actual inhabitable ranges.

Species range data are summarized in both linear (Table 5) and area (Table 7) terms. For the 28 restricted range endemic camaenids, the linear ranges vary from 0.1 to 6.1 km (median 1.65 km), and the area range from 0.01 to 7.45 km^2 (median 0.825 km^2). These area estimates are much greater than the actual inhabited areas, since much of the limestone masses are domed rock with neither fissures nor rubble heaps, and thus provide neither shelter nor feeding areas for the snails. Even with this overestimation of range areas, these species provide an astounding example of *in situ* speciation resulting in microgeographic species ranges.

Boundaries between many species do not correspond with breaks in rock masses. In the North Ningbings, *Ningbingia bulla, N. dentiens, N. laurina, N. octova, N. res,* and *N. a. australis* share the same mass (Map 17), with only *N. a. elongata* isolated. The first five species show some sympatric overlap (Table 8). The Central Ningbing Range (Map 20) is broken up into a greater number of separate rock masses. Known ranges of *Turgenitubulus* species are mostly composed of allopatric rock mass clusters. The South Ningbing Range (Map 23) shows a variety of distribution types. *Cristilabrum buryillum* and *C. simplex* live on several rock masses; *C. monodon* occupies one mass by itself, then shares the main southern mass with two other species, *C. primum* and *C. grossum* in allopatric succession (Map 24).

There are seven examples (Table 8) of microsympatry among two species, and one involving three species. The degree of overlap varies from 4.5% to 100% of known ranges. Anatomical differences in structures among such sympatric species provide the strongest evidence that different species are present.

In discussing creation of biotic reserves to preserve species or communities, the focus continues to be on comparatively large areas. Whereas 50,000 km^2 may be a "restricted range" for a species of vertebrate, the evidence presented below demonstrates that areas of less than 1 km² can cover the entire range of land snail species. A refocus of interest in establishing reserves to include such restricted range taxa may enable conserving not only land snails, but many plant and arthropod taxa. These "mini-reserves" could be established at a fraction of the cost involved in salvaging larger areas.

INTRODUCTION

The land snail family Camaenidae dominates the terrestrial mollusc fauna of the Kimberley Region in terms of both species numbers (Solem, 1985b: 975-976) and shell size (up to 35 mm in diameter). Although 143 species and subspecies have been recorded (Solem, 1979, 1981a, 1981b, 1984, 1985b, 1988), probably the species total will be doubled by adequate collecting. They show a pattern of reproductive maturation and seasonal variation (Solem & Christensen, 1984) that is well adapted to the monsoonal climate of the Kimberley. In addition, there are species interactions (Solem, 1985a) that can profoundly alter both shell and feeding structures.

Many of the species are highly localized in occurence, but in most areas collecting has not yet been detailed enough so that actual linear or area ranges can be calculated. The genera *Westraltachia* Iredale, 1933, *Mouldingia* Solem, 1984, *Ordtrachia* Solem, 1984, and *Prototrachia* Solem, 1984 from the East and South Kimberley (Solem, 1984: 702, Table 75) show a variety of linear patterns. Eleven species have a less than 10 km linear range; 12 species a linear range of 11-25 km; four species with 30-40 km linear range; and only two species with scattered, isolated populations extending a total of 120-160 km. These observations indicate that short range speciation does occur among camaenids.

The discovery that there is an endemic radiation of three genera resulting in at least 27 local very short range species, which has occurred in two sets of limestone hills covering less than 35 km² of exposures, is thus remarkable, but probably not unique. The linear ranges of these species is 0.1-6.1 km (median 1.65 km) and the area range is 0.01-7.45 km² (median 0.825 km²). The genera *Ningbingia* Solem, 1981, *Turgenitubulus* Solem, 1981, and *Cristilabrum* Solem, 1981 are restricted to and have radiated within the Ningbing Ranges and Jeremiah Hills, located in the northeast corner of Western Australia, north of Kununurra and between the east bank of the Ord River and the Northern Territory border (Maps 1, 14).

First sampled by the author in 1976, several descriptive papers (Solem, 1979, 1981b, 1985b, 1988) have named the taxa, recognized the restricted distributions of the generic and species units, and worked out the patterns of genital variation. The present paper summarizes the distribution of all land snail species known from the Ningbing Ranges, Jeremiah Hills, and surrounding areas, analyzes the range patterns of the short range restricted species within the two limestone hill areas, and discusses the general significance of this discovery to conservation biology and reserve formation.

This should be read in conjunction with other papers in preparation on the general patterns of anatomical and shell structure variations, size and shape differences within and among populations, allozyme variation and patterns, and hypothesized evolutionary divergence and extralimital affinities. These are in cooperation with Lee-Ann Hayek and David S. Woodruff. Together they will provide an overall summary of what is undoubtedly one of the most remarkable evolutionary microcosms yet discovered.

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The maps prepared from aerial photographs to show distributions in relation to exposed limestone (Maps 17, 18, 20, 21, 23) were produced by the team of Illustrator Linnea Lahlum and Associate Dorothy Karall. Maps 1 and 14 were rendered by Collection Manager Victoria B. Huff, who also helped enormously in working out the final species range data and in manipulating rainfall data.

The remaining maps were prepared using the FLORAPLOT program at the Western Australian Wildlife Research Centre, Department of Conservation and Land Management, through the courtesy of Dr. Andrew Burbidge, Principal Research Officer. The assistance of Paul Gioia, Wildlife Research Centre, who developed the program, taught me how to operate it, and supervised the entry of my data base, is gratefully acknowledged. Final touch up details on the maps were done by Victoria B. Huff and Linnea Lahlum.

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MATERIALS AND METHODS

I have had four visits to the Ningbing Ranges and Jeremiah Hills, which can be separated by the station numbers. They are:

9-12 November 1976	WA-225 through WA-237
16-19 May 1977	WA-425 through WA-435
16-28 May 1980	WA-601 through WA-676
15 June 1980	WA-700 through WA-706
22 May through 4 June 1984	WA-980 through WA-1049

The first two trips were basic exploration, learning that there was a remarkable fauna and attempting to sample quickly before moving onto other areas. Despite severe time limits, 18 of the 28 currently known restricted range camaenid taxa were collected during the 1976-7 visits. The 1980 trip was designed to work out species limits and transition patterns along the range, fill in collecting gaps along the east face, and try to reach other areas. Unfortunately, 1980 was a year in which the cane grasses reached over 3.5 meters in height. Attempts to collect to the west of the main hills were thus very difficult and frustrating. Our success in knowing where we were, plotting localities, and finding our way out again, was due to the navigational skills of Fred Aslin. Despite the operational difficulties, an additional seven species were found. The 1984 trip was designed to sample both surrounding ranges and previously unreached portions of the Ningbing Ranges and Jeremiah Hills by helicopter, and then to use ground transport to collect and prepare material of all previously known species for electrophoretic analysis. Two new species of *Cristilabrum* from the Central and South Ningbing Ranges, *Ordtrachia elegans* from an eastern outlier of the Jeremiah Hills, and several new taxa from surrounding hill systems were collected (Solem, 1988).

The individual collecting strategy on all trips was to gather a sample of live adult specimens adequate in number for dissection; to take these from as small an area as possible by identifying nodes of abundance; to take dead adult examples for variational analysis as they were uncovered in the search for live adults; to leave live juveniles alone; to pick a few dead juveniles for use in studying shell protoconch sculpture; and to try to rebuild the disturbed rubble heap so that the population would continue and rebuild the population numbers.

The initial 1976 collections, made in the very late dry season, and then the 1977 collections, made early in the dry season, demonstrated that live examples required considerably more effort to find in the late dry season. Hence subsequent field work was concentrated in May and June.

Materials

Collections of the restricted endemic genera, *Ningbingia, Turgenitubulus,* and *Cristilabrum,* totalled 16,134 adult specimens, of which 2,325 (14.41%) were taken alive. There was little difference among the genera, with 651 (15.3%) live *Ningbingia* (7 taxa), 754 (13.37%) live *Turgenitubulus* (8 species), and 920 (14.72%) live *Cristilabrum* (12 species). The range among species was larger, with a low of 7.12% (of 323) live adults for *C. isolatum* and a high of 31.73% (of 208) for *C. buryillum.*

Specimens of all three genera tend to be highly clustered. At 57 stations there were 14 or more live adults collected, often with many dead adults also present. The average number of live adults in these larger samples was 27.4 (22.2%), with 95.8 dead adults (77.8%). A total of 7,023 specimens (average 123.2) was taken just at these locations.

These prolific stations showed a combination of some shade to retard evaporation, some vegetation nearby to provide leaves as food, and rubble piles or crevices located above the plains level. An equally important criterion was that these sites would be visible to a collector. Experience soon focused collecting effort on these more likely spots. Frequently such places would be separated by 10 to 100 meters of bare rock, or by tantalizing 5 cm wide fissures in 10 meter high cliffs or boulders — with any snails well out of reach.

Methods

In the field, stations were plotted on the 1:100,000 Carlton or Knob Peak map sheets during 1976, 1977, and 1980 trips, and grid references worked out. All stations were then plotted on the aerial photographs during the 1984 field work. For most stations, the location probably is accurate to within 50 meters. Subsequent to the field work, all grid references were converted into latitude and longitude to a level of seconds.

Species decisions were based on anatomical structures and correlated conchological differences. Congeneric sympatric species showed obvious differences in terminal genital structures that correlated with often fairly minor shell changes. These situations enabled judging the probable relationship of allopatric populations. The patterns of these variations will be reviewed elsewhere.

All species records from the systematic accounts of the camaenids (Solem, 1979, 1981a, 1981b, 1984, 1985b, 1988) and the non-camaenids from the Kimberley and Northern Territory (Solem, In press — A) were entered into the FLORAPLOT program at the Fish and Wildlife Research Centre, Wanneroo, Western Australia. This program plots species records with one second accuracy. The area to be covered ranged from all of Australia down to an area a few seconds square. Maps 2-13, 15-16, 19, 22, and 24 were prepared by this program. They delineate the range of each species and show the patterns of microsympatry.

In a separate process, the aerial photographs were used to trace outlines of the limestone exposures, stream channels, and the main access track, then to locate the collecting stations along the limestone masses. Photographs were available for almost all of the Ningbing Ranges, but not for the Jeremiah Hills. Map 14, developed from the 1:100,000 map sheets, also outlines the approximate areas covered by the detailed sections in Maps 17-18, 20-21, and 23. Map 25 of the Jeremiah Hills and surrounding areas, also was developed from the 1:100,000 topographic sheets. Map 1 serves as an introduction to the Western Australian localities mentioned in the text.

A combination of grids and individual measurements were used to estimate the area of exposed limestone from which each species was known on maps 17-18, 20-21, 23, and 25. The resulting figures are approximations. Most of the limestone is not suitable habitat for snails, and the actual areas lived in will be a small percentage of the hillsides. Yet this is the nearest I can come to giving an estimate of species range. The premise has been that if a species has been recorded from one portion of a limestone mass, it probably occupies the entire mass — unless a different species has been collected elsewhere on the same hill. Especially in the Central (Map 20) and South Ningbing Ranges (Map 23), there are many additional limestone hillocks that need to be collected before range areas can be exactly determined. It is in some of these unvisited areas that additional new species may be found. The exposed dome areas above Four Mile Creek (Map 23) and much of the limestone inThe Pillars (Map 21) offer poor snail habitat, but additional species of camaenids undoubtedly exist in the Ningbing Ranges.

Data on rainfall were obtained from the Bureau of Meteorology in the form of daily records for several years, or monthly and annual summations for longer periods. Missing and incomplete records for some stations limited the number of detailed comparisons that were possible. They did permit trying to develop a method of indicating the amount of activity time available to the land snails.

The camaenid land snails entered Australia from the north after the Miocene plate collision occurred (Solem, 1979). The Ningbing Ranges and Jeremiah Hills probably were hill systems exposed in approximately their current configurations (see below) early in the Miocene, prior to arrival of camaenids into Australia. These hills were thus *colonized* by the camaenids. The question of intrageneric phylogeny will be discussed elsewhere as part of the review of speciation. Possible instances of speciation by vicariance do exist. Consideration of this subject is considered to be outside the purview of this paper. No attempt is made to consider broader distribution patterns, since that requires data from many other regions of Australia.

LOCATION AND STRUCTURE

The Ningbing Ranges and Jeremiah Hills protrude from the alluvial coastal plain that forms the current E bank of the Ord River in the far NE corner of Western Australia (Map 1). Shown on few general maps, because of both their small size and slight elevation, they are the only significant limestone exposures along the NW and N coasts of WA.

Location

The southern tip of the Ningbing Ranges lies about 53 air km NNW of Kununurra, with the ranges, exposed hills of Devonian limestone, continuing 43.5 km along a NNW axis (see Map 14). They extend from the N bank of Four Mile Creek to a last small outcrop just SW of Brolga Spring, which lies on the edge of the extensive tidal mud flats forming the E shore of the Ord River delta. The exposures are broken up into five main masses (see Map 14), which are referred to here and illustrated in detail as the North Ningbing Range (Map 17), Central Ningbing Range (Map 20), The Gorge (Map 21), The Pillars (Map 21), and the South Ningbing Range (Map 23). A number of outlying limestone fragments also contain land snails, although these hillocks are much too small in size to have been named. All of these limestone hills are enclosed by the geographic coordinates 14° 53' S to 15° 19' S and 128° 34' E to 128° 42' E.

Between the southern tip of the Ningbing Ranges and the Jeremiah Hills to the SE, is a broad area of alluvial plains and black mud flats that Sandy Creek and Redbank Creek drain into (see Map 25). Two very small, less than 100 m long, isolated limestone hills rise out of the plain. WA-624 near Redbank Creek (Map 25), which has no camaenids, is 8.2 km SE, and Laurie's Bit (WA-676, WA-1020, Map 25), which shelters *Cristilabrum isolatum* Solem, 1985, is 9.2 km SSW. Otherwise there is a gap of some 13.6 km between the South Ningbing Range and the NW outliers of the Jeremiah Hills. The Jeremiah Hills and their outlying exposures can be included within an equilateral triangle whose sides are 8.4 km long. The northern and western sides have considerable exposed limestone, but the southeastern side consists of open plains only. There are a number of very small, scattered limestone hillocks in the central and northern portion, too small for recording on even the 1:100,000 map sheets, that have not yet been sampled for snails. The whole area is enclosed by the coordinates 15° 24-29' S and 128° 44-48' E.

Current drainage of the area is varied. The South Ningbing Range and the Jeremiah Hills, as well as the sandstone Weaber Ranges to the NE, have small seasonal streams — Four Mile Creek, Redbank Creek, and Sandy Creek plus unnamed tributaries — that flow into and then are swallowed by the alluvial and black mud soils that start at Point Spring, Weaber Ranges and continue S across the Weaber Plain to the agricultural fields near the Kimberley Research Station and Kununurra. The northern portion of the South Ningbing Range and much of the Central Ningbing Range drain to the NNW into the Ord River — Surprise Creek on the E that passes through The Gorge to become Station Creek — and Mistake Creek on the W face (Maps 14, 20-21, 23). The N part of the E face of the Central Ningbing Range, plus much of the E face of the North Ningbing Range (Maps 14, 17, 18, 20), drain into the Ord River through Tanmurra Creek to the S and an unnamed creek lying just to the N. Both of these creeks pass between the Central and North Ningbing Ranges. There are no well defined creeks that drain the W face of the Central Ningbing Range.

A number of very small creeks drain the W slopes of the North Ningbing Range (Map 14) into the Ord River, while the upper E face of the North Ningbing Range drains into the mud flats fronting Joseph Bonaparte Gulf. One of these creeks passes within a few meters of Sta. WA-705, the northernmost exposed limestone inhabited by *Ningbingia bulla* Solem, 1981, and continues into the mud flats to the E of Brolga Spring (Map 14). The latter is a probable freshwater lens situated on the edge of the Joseph Bonaparte Gulf mudflats.

At one time, the main channel of the Ord River probably ran E of the Ningbing Ranges, following, in part, the route of Eight Mile Creek (Plumb & Veevers, 1971). The latter lies SE of the Sorby Hills (lower right corner of Map 14), extending from near Kununurra and the Burt Range northeastwards past the Pincombe Range into the Keep River and eventually into the Northern Territory, emptying into the Turtle Point arm of Joseph Bonaparte Gulf. There is some indication that the E face of the Ningbing Ranges was subject to probable Miocene wave erosion (R. J. Lee, personal communication). No data are available concerning the actual past drainage patterns.

Structure

The Ningbing Ranges and most of the Jeremiah Hills are composed of the Upper Devonian Ningbing Limestone. It ". . . is a reef complex in which four facies are recognized: reef (massive recrystallized limestone); fore-reef (breccia, conglomerate, calcarenite); back-reef (well-bedded calcarenite, birdseye limestone); and inter-reef (platy red and grey limestone)" (Plumb & Veevers, 1971: 15-16). This is essentially the same basic formation that crops up sporadically near the Behn River, Lissadell Homestead, then S to Nicholson River as small hills, reappearing along the S edge of the Kimberley as the relatively massive Lawford, Laidlaw, Emanuel, Home, Pillara, Oscar, and Napier Ranges (Solem, 1984: 631-634, figs 159-162). Originally this was a combined barrier-fringing reef that surrounded the Kimberley Block. The western and northern segments were subtended in the mid-Mesozoic (P. E. Playford, personal communication), while the eastern side has been subject to periodic erosion and/or burial by alluvium.

Wherever these limestones are exposed today, they are inhabited by a large number of land snails. The rocks fracture easily into talus heaps and the larger blocks show many fissures. The deep crevices provide excellent moisture retaining shelter niches.

Strong habitat contrast is provided by non-limestone rocks in the same areas. Hill systems to the east of the Ningbing Ranges, including Opir Hill (Maps 14, 20), Buryill Point (Maps 14, 23), and Knob Peak (Maps 14, 17), are quartz sandstone of Lower Carboniferous (Point Spring Sandstone) or Upper Carboniferous (Border Creek Formation) age. These expand into a major hill system connected to the much larger Weaber Ranges to the E (see Map 25). Except for the S facing and rather heavily vegetated higher cliffs of the Weaber Ranges, which are inhabited by low numbers of *Torresitrachia weaberana* Solem, 1979 (Map 12), *Westracystis lissus* (E. A. Smith, 1894) (Map 4), *Stenopylis coarctata* (Moellendorff, 1894) (Map 5), *Gastrocopta* species (Map 6), and *Eremopeas interioris* (Tate, 1894) (Map 8), these formations are essentially "snail-free". The few exposures of sandy and silty Upper Devonian limestone known as the Buttons Beds are in the Sorby Hills, Eight Mile Creek area, and bed of the Ord River N of Ivanhoe Crossing (Plumb & Veevers, 1971: 16). They are not good snail habitats, although the Sorby Hills (WA-667, WA-1040) yielded a representation of the dry open country small species and *Torresitrachia weaberana* (Map 12).

Almost nothing is known concerning the Tertiary history of the Ningbing Ranges. Geologists familiar with the area are willing to state that the Ningbing Limestone has been exposed at least since the start of the Miocene, that alluvial plains have been built and eroded during changes in sea level, and that the Ningbing Ranges may have been exposed in very much their present configuration since the early Miocene (Lee, Playford, personal communications). Probably there has been only a few meters reduction in emergent height of the ranges since the early Miocene, caused by the most recent buildup of the alluvial plains. Prior to completion of the Ord River dams, there is anecdotal evidence that occasionally there was flooding of the Ningbing Ranges to a significant depth. Solem (1981b: 323) recorded collecting a cluster of long dead examples of the freshwater viviparid *Notopala essingtonensis* (Frauenfeldt, 1862) in a dirt filled pocket on a limestone cliff about 7.5 m above the present floodplain. Presumably these were carried by flood waters, stranded there when the flood subsided, died, and were buried subsequently. With the dams now in place, such flooding will not recur. These past floods could have provided occasional accidental transport of snails between limestone masses.

HABITAT PARAMETERS

The Ningbing Ranges and Jeremiah Hills are centered in a relatively dry trough between two very wet regions — the Darwin area of rain forest to the E, and the Kalumburu-Mitchell Plateau-Kimbolton rain forest to the W. All these areas have a monsoon climate, with heavy summer rains between late October and March (Table 1), but the differing quantities of rainfall are reflected in dramatic changes of both vegetation and fauna.

Moisture availability

There are no rainfall gauging stations in the Ningbing Ranges. The nearest ones (Map 1), Carlton Hill Homestead (ca 22.5 km SW of the South Ningbing Range tip) and Ivanhoe Station (ca 11 km NW of Kununurra), probably give a reasonable approximation of total rainfall and number of rain days in the region. Including the more recent records supplied by the Kimberley Research Station (ca 5 km NE of Ivanhoe Station) and Kununurra itself in Table 1 serves to point out how the number of rain days can differ dramatically over a short distance. Lissadell, further S on the SE shore of Lake Argyle, is listed since it has limestone exposures with camaenid land snails present, while the far inland Halls Creek lies on the SE margin of the Kimberley Block, below the recorded limit for camaenid snails.

It is not adequate to describe land snail and moisture regime interactions only in terms of annual rainfall and number of rain days. The data in Table 1 thus has been organized to reflect some basic limitations that moisture availability places on land snails in terms of activity. Near 100% humidity is required if water loss from their body is to be restricted to a tolerable rate. In the absence of abundant moisture, activity is possible at peril of their lives. During the dry season, land snails aestivate. Even during the wet season, moisture availability is sporadic, and snail activity must be correlated with available moisture. There will be periods of several days to a few weeks in which the snails will suspend activity and resume aestivation. The rate of evaporation after a rainfall will be quite rapid on the surface, slower in a rock pile exposed to the sun, much slower in a shaded rock pile, and extremely slow in a deep fissure where water slowly seeps inward and downward. The top and base of a rock pile will become dry several days apart. Thus a "rain event" will permit different periods of activity for different populations of snails on the same hill. It is thus extremely difficult to establish correlative parameters regarding "the snails" on a multi-faceted hillside with varying degrees of evaporative water loss.

Table 1 attempts to deal with this problem in a preliminary way. On the basis of chance observations in the Napier Range and the Cape Range, where I was at localities when a "first rain event" happened, some comments and predictions can be offered. In the Cape Range, there had been a rain in excess of 53.8 mm on 1 January 1974, possibly as much as 75 mm. Yet when I started collecting at Goat Cave on 16 January, there was no trace of snail activity. All live specimens collected had epiphragms in place. During that night there was a brief thunderstorm, which also fell on Ningaloo Homestead to the S. It registered there as 17.2 mm. Normally, according to owner Edgar Lefroy (personal communication), there is about 50% more rain on the Cape Range than at the Homestead (based on several years in which a gauge was maintained by the Lefroy's on the W slope of the Cape Range). I thus estimate that probably 25 mm of rain fell where we were camped. This was followed by three nights of snail activity, two with hundreds of active individuals, the third with reduced activity.

On 5 December 1976, at Napier Downs station in the Napier Range, a late afternoon thundershower from the NE lashed the Homestead and E facing valley sides of the Napier Range S face with 18 mm of rain in about 15 minutes. The previous wet season had ended with 9 mm of rain on 21-22 March; early drizzles of 4 mm on 26 September and 6 mm on 21 October preceeded the 5 December fall of 18 mm. This latter shower activated snails in crevices on the E facing slopes within 15 minutes, but the W facing slopes received no rain and there was no sign of snail activation. A gentler fall of 10 mm on 6 December resulted in snail activity on both sides of the valleys. It is probable that brief showers, producing only a few mm of rain, will not penetrate far enough into talus or deep fissures to activate aestivating snails. A rain of 10 mm or more will activate most populations, and 8 mm of rain is good for about "one snail night" of activity.

Thus I have, somewhat arbitrarily, selected a 10+ mm rain to mark both the beginning and the end of the wet season, and refer to rains over 10 mm as "significant falls". To emphasize that the rain is not continuous during the wet season, I also have recorded the dates for the second fall and then the "next to last" rain for each locality, given the range observed over a several year period, as permitted by available data, and then averaged the various dates. Because other data is based on a calendar year, I have calculated wet season on a "within the same year" basis. It would have been more accurate to use "actual wet season" length from its start in October of one year to its termination in March or April of the next year, but I balked at redoing all rainfall calculations to conform to seasonal realities.

There is considerable annual variability (Table 1) as to the start of the wet season, although the average date clusters between 17 October and 5 November for all stations except Halls Creek. The end of the wet season clusters in early to mid-April, except for the earlier date at Lissadell. Normally there is a significant gap between "first and second" and "next to last and last" falls. Again excluding Halls Creek, the mean gap is 15.8 to 19.4 days between "lst and 2nd", then 10.4 to 19.4 days between the "next to last" and "last" significant rains. The range of days between these pairs of events is very large.

In a practical sense, an aestivating snail, that was prepared to function as a male, could be activated by the first rain, feed, mate, and during the "time gap" from "1st to 2nd" rain, fertilize and encapsulate eggs, using energy obtained from the food taken in during the activity period permitted by the "1st rain". Exactly this type of reproductive strategy has been hypothesized by Solem & Christensen (1984). Thus the time gap at the start of the wet season may have been incorporated into the reproductive cycle of the snails.

Excluding Lissadell, the average length of the wet season is not spectacularly different, clustering between 151 and 185 days. The "heart of the wet season", here defined as the period between the "2nd rain" and the "next to last" rain, is 154 days for the very wet Mitchell Plateau, but only 103-135 days at the E Kimberley stations. Number of rain days also varies greatly, both from year to year and over the short distances in the Carlton Hill-Kununurra area.

The average and median annual rainfalls (Table 1) vary considerably among the stations. Mitchell Plateau, with an annual average of 1593 mm, receives twice as much rain as Carlton Hill. Darwin, Northern Territory (12° 25′ S, 130° 52′ E) has averaged 1479 mm/year during 70 years of record keeping. Of this, an average 1300 mm falls between November and March. In the Carlton Hill to Kununurra area, the median annual rainfall drops down to a range of 726 to 797 mm. The effects of one or two very wet years are clearly shown by the uniformly higher mean than median rainfall at these stations — 1968 and 1969 had 1442 mm and 1043 mm at Carlton Hill, but only 398 mm in 1970; Ivanhoe recorded the same pattern, but in 1974 also had 1170 mm (1974 records for Carlton Hill are incomplete, so the rainfall total for that year is not available). The period from 1974-1984 was much wetter at Lissadell and Halls Creek than the 1951-1976 interval. There are both annual and short term fluctuations in rainfall, as demonstrated by the wide ranges recorded at each station.

Given these fluctuations, raw annual data clearly are inadequate in defining moisture availability for land snails. The limestone of the Ningbings retains moisture far better than does the sandstones around Kalumburu and Mitchell Plateau. But the nearly doubled *amount* of rainfall, delivered essentially in the same amount of time (Table 1), supports a much more varied and luxuriant flora and more diverse land snail fauna in the W Kimberley.

At least in regard to the semi-arid to arid areas, a perhaps more useful way to look at moisture availability to land snails is in terms of "snail activity nights" (SAN). This becomes particularly striking when a semi-arid area, such as Ningaloo station at the SW end of the Cape Range is analyzed. Between 1974 and 1984, the recorded total annual rainfall ranged from 102-451 mm (mean 272.3 mm), and the annual number of rain days varied from 22-45 (mean 30.5). The estimated number of *snail activity nights* allowed by the rains was only 6.5-44.5 (mean 24.8). A *snail activity night* is provided by 8 mm of rain. Multiples of that increase the number of "active nights", *i.e.*, 32 mm of rain would support four nights and 56 mm would support seven nights of activity. There would be diminishing returns as the amount of rain increased, since the extra water would run off from the snail inhabited hillsides. I doubt that rains of 75-100 mm would effectively prolong the period of snail activity. Rains falling on consecutive days, or when the "new" fall comes *before* the projected activity period has lapsed, are counted here as representing a single "event". In the Cape Range, such events are scattered over eleven months of the year. Only December failed to show a SAN from 1974 through 1984. The maximum number of such events for any month occurred in May (9), with June (8), March and July (7), August and February (6), and April and January (4) combining to account for 51 of the 57 "events" in eleven years. The annual average of such events is only 5.2 (range 2-8). The Cape Range is a floristically and malacologicaly rich area compared with other sections of the W coast of WA, yet the land snails would average 5.2 "activations" per year for a total of 24.8 SAN's. The Cape Range has no "wet season". The comparatively little rain it does receive comes as occasional drenchings, yet the land snails flourish. Low lying coastal areas to the S benefit from occasional ocean fogs rolling inland and providing condensation water to supplement actual rainfall. The number of such fog episodes is not known to me and I also do not know if such fogs penetrate into the heart of the Cape Range. The above items may increase the moisture availability somewhat, but the basic pattern will be little altered.

The above analysis is especially appropriate to an area with sporadic and aseasonal rainfall. It focuses on the extremely limited activity time provided by even heavy showers. Applying this analysis to the Kimberley, with its marked seasonality of rainfall and much larger amounts of rain, is more difficult. The number of storms occurring in the heart of the wet season can result in almost continuously moist conditions, and the concept that 8 mm rain = one snail activity night may have less validity. The denser vegetation in the Kalumburu-Mitchell Plateau area would retard evaporation rates, but the concept of less than full time activity patterns would hold.

Despite these caveats, it is very instructive to compare the conditions during "average" wet seasons at the Mitchell Plateau and Carlton Hill station. Because the data set is incomplete for

Carlton Hill, it was not practical to compare the same wet seasons. And, to give a more realistic comparison, data from October of one year through March of the next year, rather than same year data, have been used for the sample wet seasons. This gives an actual wet season period, rather than the "parts of a year that are wet" analysis used above for convenience. The basic data are:

	Annual averages		Sample period		
	Mean Rainfall	Mean days in wet	Year	Rainfall in wet	Days in wet
Mitchell	1593 mm	185	1975-6	1769 mm	194
Carlton	776 mm	151	1971-2	822 mm	158

Since both wet seasons are slightly wetter and longer than the means, this is a fair comparison. At Carlton Hill, there were 12 "rain events" providing 78 "snail activity nights" (SAN); at the Mitchell Plateau, there were 20 rain events producing 104 SAN. During the "heart of the wet season" (here defined as period of most concentrated rainfall) at Carlton Hill (21 November through 18 March) there were 71 SAN (60%); and at the Mitchell Plateau (1 January through 28 February) there were 45 SAN (75%). In the combined start and end periods of the wet season at Carlton Hill (8-20 November and 19 March through 13 April), there were only 7 SAN (18% of 39 days); at the Mitchell Plateau (9 October through 30 December and 1 March through 19 April), much more activity was possible, with 59 SAN (44% of 134 days). At Carlton Hill, the four best months for snail activity were November (11 SAN), December (17), February (19), and March (18); at the Mitchell Plateau the equivalent figures were December (18), January (22), February (23), and March (22).

Despite sharing the same basic monsoonal climate, and usually exposure to the same cyclonic storms, snails living on the Mitchell Plateau can be somewhat more active (25%) in the heart of the wet season, and much more active (144%) during the beginning and end of the wet season than can snails living near Carlton Hill. The limestone rocks in the Ningbings may extend the activity periods somewhat, but there are real differences in opportunity for being active that correlate with the different patterns of precipitation.

The sheer quantity of rainfall at the two places also makes the fate of streams and pools very different. The streams on the Mitchell Plateau mostly maintain at least a trickle flow even near the end of the dry season, and there are major permanent pools of water. During the wet season, the streams become impassable raging torrents. In the Ningbing Ranges, the streams flow through much of the wet season, are reduced to isolated pools early in the dry season, and mostly dry out by the middle of the dry season. Brolga Spring (Map 14) is the only significant permanent body of water. It is fed by seepage through the mud and alluvial plains and probably is a lens of freshwater on top of a brackish water base. Brolga Spring has a fringe of palms and other wet area plants, in part certainly natural, but possibly supplemented by residents during the periods when Brolga Spring functioned as an outcamp for the former Ningbing Station. It is a wet oasis during the dry season and harbors some wet area land snails (see below).

In simple summary, no understanding of the semi-arid area land snails is possible without realizing the extent to which their periods of activity are limited by the unavailability of moisture. Contrasting the three areas discussed above, the Mitchell Plateau, receiving an average of 1593 mm of rain, has a dry season of 171 days (in which no snail activity occurs) and probably an additional 90 days DURING the wet season in which activity in the average rock pile or crevice must be suspended — for a total of 261 days (71.5%) without activity. At Carlton Hill, which receives an average of 776 mm of rain, the dry season is 207 days, plus an additional 80 days of suspended activity during the shorter wet season, for a total of 287 inactive days (78.6%). At Ningaloo, there is no wet season, and the average annual inactivity time is estimated at 340 days (93.2%).

The above summary figures also demonstrate that, once a land snail is adapted to a monsoon climate, where there are dependable long periods in which aestivation is necessary, adjustments to semi-arid or arid conditions probably are minor accomplishments — the rise from 71.5% to 93% inactivity days.

Vegetation

There are neither vine thickets nor rain forest patches in the Ningbing Ranges and Jeremiah Hills. While patches of black mud, in particular, are capable of bogging vehicles well into the dry season, and soft patches exist through most of the dry season, there are no swamps or *Pandanus* — except around the fringes of Brolga Spring, which is well removed from the limestone outcrops. There are no cycads, nor *Livistona* palms. There are no closed forest conditions. Basically they have savannah type cover with stands of tall grass and numerous scattered baobab trees (*Adansonia*). Rarely are there large trees of other species growing from the rock crevices that can provide falling leaves as food for the snails.

The contrast with the Mitchell Plateau and its 649 species of plants and 14 structural formations (Hnatiuk & Kenneally, 1981), many stands of dense rain forest and vine thicket, hillsides with cycads, often nearly closed forests with *Livistona* palms, and swamps is stark.

Recent years have seen increased pyromaniac tendencies among inhabitants of the Kimberley. Casual dry season fires started by flicking lighted matches into dry grass clumps (early 1970's) have been replaced by deliberate fire bombing of extensive areas. In 1984, the sky over the Ningbing's was blackened by smoke clouds and we had to shift collecting to other areas during the worst of the blazes. Fortunately, those snails in deeper talus will survive all but the largest fire storms. Unquestionably, this substitution of annual, whole area burning for the historical partial burns, and the pre-human habitation pattern of major blazes at irregular intervals, will have considerable effect upon the vegetation diversity and cover.

Snail occurrence

Land snails in the Ningbing Ranges and Jeremiah Hills are not randomly distributed. Most species are highly clustered and limestone associated, whether it is in the main masses or under loose blocks or in crevices of half meter high exposures. The primary exception is *Xanthomelon obliquirugosa* (E. A. Smith, 1894). Although low numbers of dead shells have been collected from limestone localities throughout the North and Central Ningbing Ranges (Map 7), *Xanthomelon* probably is basically a plains dweller that burrows into the soil to aestivate (as do its relatives near Darwin).

On the limestone masses themselves, limestone rubble accumulations at the base of cliffs, bottom of horizontal or vertical crevices, and even small rock piles by the side of boulders on an otherwise barren slope are apt to be aestivation sites for camaenid land snails. All of the Ningbing-Jeremiah camaenids are "free sealers", that is, the shell aperture is closed by a sheet of calcified mucus, with the shell lying loose in litter, rubble, or on the soil surface. Occasional juveniles will be found sealed to a rock surface or to another shell, but the adults never attach during aestivation. The other two restricted endemic species, *Georissa* species (Map 3) and *Gyliotrachela ningbingia* Solem, 1981 (Map 2), are found sealed to rocks in rubble not buried by soil, most commonly in the small hemispherical pits on the rock surface or in small crevices or fractures. The large number of stations recorded for these two species reflects the fact that in removing rocks from the top of the talus in order to reach the level of live camaenids near the bottom of the pile, these small, colourful (*Georissa* orange-yellow; *Gyliotrachela* purplish-brown) snails are readily spotted. *Westracystis lissus* (E. A. Smith, 1894) (Map 4) seals to rocks or leaves (Solem, 1982: 187, figs 12-13), and sometimes *Gastrocopta* sp. (Map 6) or *Pupilla pacificus* (Pfeiffer, 1846) (Map 9) will be found sealed to rocks. The other genera (*Stenopylis*, Map 5; *Eremopeas*, Map 8; *Discocharopa*, Map 11) found in the limestone areas are litter dwellers. One species found on the fringes of the limestone masses, *Torresitrachia weaberana* Solem, 1979 (Map 12), is a litter or rubble dweller that free seals. Several taxa that occur on the wet margins of Brolga Spring (*Pupisoma orcula* [Benson, 1850], Map 10; *Pupisoma* sp., Map 10; *Coneuplecta microconus* [Mousson, 1865], Map 11; *Nesopupa mooreana* [E. A. Smith, 1894], Map 11) are mostly litter dwellers that will forage on bark during activity periods, although *Pupisoma* does aestivate in crevices of rough barked trees (Vince Kessner, personal communication). No live *Austrosuccinea* have been taken in the Ningbing Ranges. In a watered garden on the Kimberley Research Station grounds (Sta. WA-1049, FMNH 211926) specimens were live in litter at the base of a tree. In the Red Centre, *Austrosuccinea* (= *Succinea* and *Arborcinea*) aestivates sealed to started bark on large river gums by stream banks. George W. Kendrick (personal communication) has found it among cane grasses on the black soil flats near Barker Gorge, Napier Range.

The dominant camaenids can aestivate at any level of a rock pile or crevice. Those near the top run the risk of being baked during the dry season, and late dry season sampling (November 1976) resulted in finding many examples with dried soft parts intact. Collecting early in the dry season (May and June) finds these still alive, and the collector is, in effect, cropping doomed individuals when these live snails are taken for research study. The mass of live individuals will be found deeper in the piles, but above the level silted in by dirt. The latter "graveyards" may contain hundreds to thousands of empty shells, many with epiphragms or epiphragm fragments still in place.

Those snails near the top of the pile could be activated by even light showers, but run the risk of drying out between wet seasons. Those at the very bottom of a pile may become buried by flood silt and die. Those just above the silt level will have maximum activity periods.

The area required for a successful colony of camaenids to persist seems to be incredibly small. For example, Station WA-700 in the North Ningbing Range (Map 17), was a pocket of rocks about two feet in diameter and two feet deep, situated on the south side of a large (8 feet high) boulder perched about 5 meters up from the alluvial plain on a slanted slope that was barren of vegetation. This "pocket" yielded 60 live and 175 dead adults of *Ningbingia dentiens* Solem, 1985 and 18 dead adults of *N. laurina* Solem, 1979 — even though much of the colony was left unexcavated to ensure survival of the colony. The boulder provided shelter from direct insolation; the barren slope prevented significant soil accumulation that would silt up the pocket; the small rocks had a warren of crevices through which the snails could move and plenty of room for aestivation; and leaves blown against the boulder by winds would drift into these crevices, providing food for the snails.

COMPOSITION OF THE FAUNA

At present, 43 species of land snails are known from the Ningbing Ranges and Jeremiah Hills (Tables 2, 4). Thirty are found nowhere else in the world. Of these, three belong to genera with wider distributions; 27 to genera found only in these ranges. The remaining 13 species (Table 2) also are indigenous, but have extended ranges. A number of other species come close to, but do not reach the ranges, and additional taxa in the hills to the east, west, and south serve to define the Ningbing fauna by their absence.

Two species are restricted to, but generally distributed within, the Ningbing Ranges and do reach the Jeremiah Hills. The prosobranch genus *Georissa* Blanford, 1864 ranges from Japan and India to Hawaii and the Austral Islands. It is fairly common in Indonesia, especially Borneo, and rare in New Guinea. The only other Australian records are from near coastal Queensland and northern New South Wales (see Solem, In press — A). The Ningbing Range species, *Georissa* new species (being described by Solem, In press — A), is one of the commonest species in the Ningbing Ranges and Jeremiah Hills, recorded from 58 collections (Map 3). It is more common in the northern sections. *Gyliotrachela* Tomlin, 1930 is a basically southeast Asian and Indonesian genus, belonging to the Pupillidae. There are only a few widely scattered Australian species (Solem, 1981c, In press — A): *Gyliotrachela napierana* Solem, 1981 from the western Napier Ranges, southwest Kimberley; *G. catherina* Solem, 1981 from the Douglas-Daly area southwest of Darwin and near Katherine, Northern Territory; *G. australis* (Odhner, 1917) from Chillagoe Caves, northern Queensland; and *G. ningbingia* Solem, 1981 from the Ningbing Range and Jeremiah Hills (Map 2), which also is more common in the northern sections.

The 28 species with restricted ranges (Tables 3-4) all have been described in the last few years (Solem, 1981b, 1985b, 1988). *Ordtrachia elegans* Solem, 1988 has been found in the easternmost outlier of the Jeremiah Hills (Map 12), where it is sympatric with two other camaenids, *Cristilabrum bilarnium* Solem, 1981 and *C. spectaculum* Solem, 1985. Its total range is about 0.32 km². Other species of *Ordtrachia* range from near the Behn River and Lake Argyle south to Nicholson (Solem, 1984: 647-670).

Ningbingia Solem, 1981 has six species and a described subspecies; *Turgenitubulus* Solem, 1981 has eight species; and *Cristilabrum* Solem, 1981 has 12 species. The overall generic distribution pattern is one of allopatry (Maps 13-14), with *Ningbingia* restricted to the Northern Ningbing Range (also Map 16); *Turgenitubulus* (Map 19) to the Central Ningbing Range, The Gorge, and The Pillars;

and *Cristilabrum* (Maps 22, 24) to a small portion of the Central Ningbing Range, South Ningbing Range, and the Jeremiah Hills area. *Turgenitubulus* apparently has evolved from *Cristilabrum*, but *Ningbingia* represents a separate phyletic unit (Solem, unpublished). All of these species have very restricted ranges, occupying only small portions of the Ningbing Ranges and Jeremiah Hills (Tables 4-5, 7). Details of their distributions will be discussed below.

The indigenous, but not restricted, taxa show a variety of affinities and distributions. They are discussed as: 1) the eight taxa that inhabit the main range; and 2) the five taxa fringing the main ranges. They are varied in both taxonomic position and ecological patterns. Details of distribution, illustrations, and a summary of ecological data are presented in Solem (In press — A) for the non-camaenid taxa. Family affinities are listed in Table 2.

The main range taxa consist of:

Westracystis lissus (E. A. Smith, 1894) (Map 4): Very common throughout area, also northwest on Shakespeare Hill. It ranges throughout the Kimberley from the Napier Range east to the Lawford Range, then north to Kalumburu and east through the Ningbing and Weaber Ranges into the Northern Territory as far as Timber Creek Police Station. It is replaced in the rest of the Northern Territory above the Roper River by *Westracystis fredaslini* Solem, 1982. It has not been found in the drier East Kimberley from Nicholson to just south of Kununurra.

Stenopylis coarctata (Moellendorff, 1894) (Map 5): This species is common in the North and Central Ningbings, then reappears in the Jeremiah Hills, Weaber Ranges, and Sorby Hills. Extralimitally, it has been found throughout the Kimberley, Northern Territory above the Roper River, in Queensland as far south as near Bundaberg, and throughout the Red Centre. To the north, it ranges from the Philippines and Indonesia to the Solomon Islands.

Gastrocopta new species (to be described in Solem, In Press — A) (Map 6): Common throughout the area. In the Northern Territory, it has been collected at Melville Island, Oenpelli, West Arnhem Land, near Mataranka, and Daly Waters. In Western Australia, it ranges in the drier east and south portions of the Kimberley, but is mostly absent from the very wet Prince Regent River and Mitchell Plateau areas.

Xanthomelon obliquirugosa (E. A. Smith, 1894) (Map 7): Present in low numbers through the North and Central Ningbing Ranges, and The Gorge. Dead examples are scattered on plains areas below the South Ningbing Range. A few individuals have been found on the margins of the Sorby Hills and Weaber Ranges, but it has not been taken in the Jeremiah Hills. Found west of the Ord River on the Lyne River (WA-985), then west to the Drysdale River, Kalumburu, Mitchell Plateau, some offshore islands and the north tip of the Prince Regent River Reserve. It has not been collected in the Northern Territory, nor from inland areas of the Kimberley. See Solem (1979: 35-42; 1985b: 921-922) for discussion and illustration of this species.

Eremopeas interioris (Tate, 1894 (Map 8): Rather rare in the Ningbing Ranges, but commoner in the Jeremiah Hills, Weaber Ranges, Sorby Hills, and at the Kimberley Research Station. Common throughout the Kimberley, with southern isolated occurrences in the Pilbara and Cape Range. Replaced in wetter portions of the Northern Territory above the Roper River by *E. tuckeri* (Pfeiffer, 1846), but present from near Port Keats east to Katherine and south to Nicholson, then common in much of the Red Centre. There are a few isolated records in western Queensland. Lives under a wide variety of moisture conditions.

Pupoides pacificus (Pfeiffer, 1846) (Map 9): Rare in the Ningbing Ranges and Jeremiah Hills. Found in the Weaber Ranges and Sorby Hills, becoming much more common inland in the East Kimberley and along south fringes of the Kimberley. It also is common in basically drier patches of the Northern Territory. In Queensland, it ranges from Torres Strait into New South Wales near Barrington Tops. It is not common in the rain forest patches of the Kimberley or Northern Territory.

Austrosuccinea species (Map 10): A very few dead examples have been found in the Ningbing Ranges. Live juveniles were taken from a watered garden at the Kimberley Research Station. Its specific identity and relationships remain unknown. There are scattered records from both the Kimberley and Northern Territory above the Roper River. Succineids are moderately common in the Red Centre.

Discocharopa aperta (Moellendorff, 1888) (Map 11): Probably rare in the Ningbing Ranges, but can be overlooked easily because of its small size. Also recorded in low numbers from many rain forest patches in Western Australia, a few Red Centre localities, and at a few localities north of the Roper River. It lives in Queensland, ranging south to the northern tip of New South Wales. Its extralimital range is from the Philippines and Indonesia through New Guinea and the Bismarck Archipelago to the Society, Austral, and Kermadec Islands.

The above species are a highly varied lot. *Stenopylis* and *Discocharopa* are Indonesian-Melanesian taxa that have managed to colonize Australia as far south as the Red Centre. *Pupoides, Gastrocopta, Eremopeas,* and probably *Austrosuccinea* are essentially drier country species of general Kimberley-Northern Territory above the Roper River distribution, one of which (*Pupoides*) also extends into Queensland and New South Wales. *Westracystis lissus* is a hardy species found from very wet to moderately dry areas, although absent from the Lake Argyle to Nicholson portion of the East Kimberley. *Xanthomelon obliquirugosa* is at its eastern distributional limit, and is basically a species of the wetter north Kimberley.

The above species do not represent a coherent faunal unit and do not show congruent tracks in the sense of vicariance biogeography. They simply are species that inhabit the Ningbing Ranges because that area occurs well within their individual ranges.

The fringing species also are reviewed in Solem (In press A):

Pupisoma orcula (Benson, 1850) (Map 10): One record from a wet patch in the Ningbing Ranges. Very rare on Mitchell Plateau and near Carson River, Western Australia, common in vine thicket and rain forest patches of the Northern Territory. Ranges from Southeast Asia to the Tuamotu Islands and South Africa.

Pupisoma species (Map 10): Found at Brolga Spring (Map 14), South Goulburn Island, and near Katherine, Northern Territory. Actual range and identity unknown.

Coneuplecta microconus (Mousson, 1865) (Map 11): Found at Brolga Spring (Map 14), scattered wet areas in the West Kimberley and Northern Territory above the Roper River, and coastal Queensland. Reported from Malaya and Indonesia, but not New Guinea, then Vanuatu, Fiji, Tonga, and Western Samoa.

Nesopupa mooreana (E. A. Smith, 1894) (Map 11): Found at Brolga Spring (Map 14), common in the Drysdale National Park, recorded on the Mitchell Plateau and near Kalumburu. Widely distributed in the Northern Territory above the Roper River.

Torresitrachia weaberana Solem, 1979 (Map 12): Found at scattered localities along the fringes of the North Ningbing Range — for example, at the base of a baobab some 20 meters from the nearest limestone by the bank of a seasonal stream (WA-633, Map 14) and in horizontal fissures on a very small limestone hillock at the southwest margin of Utting Gap (WA-994, Map 17). Common in Weaber Ranges, Sorby Hills, and near Spirit Hill by the Keep River in the Northern Territory. See Solem (1979: 84-86; 1985b: 924) for illustrations and discussions.

Two of the above species, *Pupisoma orcula* and *Coneuplecta microconus,* are Indonesian-Polynesian taxa that have extensive ranges in the Northern Territory above the Roper River, and are rare in the rain forest areas of the Kimberley. In would not be surprising if *Liardetia scandens* (Cox, 1872), which has a comparable distribution (Solem, In press — A), also is found eventually near Brolga Spring. *Pupisoma* sp. may be an undescribed species. All three of the above are "wet area" taxa from the margins of Brolga Spring or a seasonally wet area. A number of "wet area" taxa with combined Kimberley-Northern Territory ranges (Solem, In press — A) are conspicuous by their absence: *Pleuropoma walkeri* (E. A. Smith, 1894), *Elasmias manilense* (Dohrn, 1863), *Elasmias terrestris* (Brazier, 1876), *Pupisoma circumlitum* (Hedley, 1897), *Nesopupa novopommerana* I. Rensch, 1932, a new genus and species of pupillid (Solem, In press — A), *Amimopina macleayi* (Brazier, 1876), and *Wilhelminaia mathildae* Preston, 1913. The "dry area" *Gastrocopta recondita* (Tapparone-Canefri, 1883), from the South Kimberley and drier areas above the Roper River also may be discovered in the vicinity of the Ningbing Ranges and Jeremiah Hills. It is quite possible that the "center of the continent" species *Gastrocopta deserti* Pilsbry, 1917 may be found further north of its single area record at the Ord River Crossing of the Great Northern Highway (Map 6).

Torresitrachia weaberana belongs to a genus that extends from Torres Strait west to the Napier Range and Kimbolton area. In both the Napier Range and the Ningbing Ranges it is a fringe dweller, apparently, for unknown reasons, excluded from main limestone masses by other camaenid species.

The recorded fauna is thus a scattering of eight fairly dry adapted species with varying extralimital distributions; a few "wet area" taxa on the shores of Brolga Spring, just northeast of the Ningbing Ranges; one representative of a wide ranging genus, *Torresitrachia weaberana*, that is found up to, but not into, the Ningbing Ranges; two endemics common throughout the Ningbings, *Georissa*, new species and *Gyliotrachela ningbingia*, who have few (and distantly located) Australian relatives; and then the 28 restricted endemics with very small geographical ranges — *Ningbingia*, *Turgenitubulus*, *Cristilabrum*, and *Ordtrachia elegans*. Without the latter grouping, the Ningbing Ranges and Jeremiah Hills would be worth only a biogeographic footnote in a general review of the Kimberley-Northern Territory land snail fauna.

In a past wetter period, especially if vine thicket or rain forest vegetation were present, undoubtedly many of the "wet area" species now present to the west and the east would have been living in the Ningbing Ranges, making this area part of a continuous fauna extending from the Gulf of Carpenteria west to the Prince Regent River Reserve and probably further south. Some of the current "dry area" taxa might not have been present. Undoubtedly climatic shifts have altered the composition of the Ningbing land snail fauna through time.

Several taxa recorded from sandstone hills east, south, and west of the Ningbing-Jeremiah area are important in understanding the nature of the camaenid fauna. The genus *Mesodontrachia* Solem, 1985 (Map 13) is represented in the Cockburn Range southwest of Wyndham by *M. cockburnensis* Solem, 1988, and then further east by *M. desmonda* Solem, 1985 from near Desmonds Passage, West Baines River and *M. fitzroyana* Solem, 1985 from ca 20-25 km east of Timber Creek Police Station along the Victoria Highway in the Northern Territory. *Amplirhagada* Iredale, 1933, a south and West Kimberley genus, is now known (Map 12) from the Lyne River, which drains into the west side of the Ord River (*A. cambridgensis* Solem, 1988); *A. questroana* Solem, 1981 from the Salmond, Chamberlain, and Pentecost Rivers in the Elgee Cliffs-Durack Range area southwest of Wyndham; and *A. osmondi* Solem, 1988 from the Palms Yard-Bungle Bungle Outstation region in the drainages of Red Rock Creek and Osmond Creek, upper Ord River drainage, southeast of Turkey Creek. One additional genus, *Prymbriareus* Solem, 1981, from near the junction of the Pentecost and Chamberlain Rivers (Map 12) is important as representing the genus that is anatomically most similar to *Ningbingia*. The above three genera occupy the best snail habitable hills around the Ningbing Ranges. Their presence effectively narrows the possibility that any of the Ningbing genera will be found elsewhere.

SHORT RANGE SPECIATION PATTERNS

The total length of the Ningbing Ranges and Jeremiah Hills is approximately 52 km. Within that distance are packed more than 28 species of short range endemic camaenid land snails. Most species are allopatric, but there are eight areas (Table 8) of microsympatry (only one involving more than two species). The linear ranges of the species are only 0.1-6.1 km (median 1.65 km). The area of limestone apparently occupied by each species varies from 0.01 to 7.45 km^2 (median 0.825 km^2).

This radiation fills the available habitat space. There are no "vacant hills" suggesting that either: 1) ranges might be constricting and thus extinction approaching; or 2) that the radiation is too young to have expanded to the limits of available space. It is an exuberant radiation with no places left to go.

Collecting to date has demonstrated that wherever rubble piles can be found or crevices investigated, at least recently dead examples of these species will be found. A possible exception may be very small hillocks that are only a few meters in diameter. One such hillock near Utting Gap in the North Ningbing Ranges (Map 17, WA-994) had *Torresitrachia weaberana* present, but no specimens of *Ningbingia*. Time available to date has not permitted extensive sampling of outlying hillocks to try and estimate the minimum hill size needed to maintain a colony of the restricted endemic species. Such a survey would be well worthwhile.

Tables 4-8 and Maps 14-25 summarize the data on the endemic restricted camaenids. The two basic measurements used are *total linear range* and *total limestone area range.*

Linear ranges were calculated very simply. The distance between the furthest stations from which examples have been collected, or the distance from occupied limestone mass tip to limestone mass tip, was measured to the nearest 0.1 km. These were done, preferably, on the "limestone exposure" maps (Maps 17-18, 20-21, 23), but otherwise I used the 1:100,000 Carlton 4667 (Edition 1) and Knob Peak 4668 (Edition 1) map sheets on which the 1976, 1977, and 1980 stations had been plotted in the field.

East slope collecting stations are more numerous for two reasons. First is the simple matter that there is four-wheel drive access to the east slope; the west side is behind barriers of 0.5-1 meter high reef edges, dense stands of cane grass hiding 1-2 meters vertical stream banks, and black mud bogs. Thus most west slope localities were visited on helicopter trips in 1984. Second, field efforts have been concentrated on determining: 1) transition points between species; or 2) the lengths and continuity of overlap sympatric zones. In the North Ningbing Range (Map 17), for example, when stations WA-667, WA-666, WA-636 produced collections of the same two species, time was not devoted to sampling the area between WA-666 and WA-636. On the east slope below Utting Gap, stations WA-639, WA-642, and WA-643 had populations of *Ningbingia res,* while *N. australis australis* appeared at WA-644, about 0.65 km further south. The cliff face between WA-643 and WA-644 contained no easily accessible rubble piles in which to collect. Thus this gap in sampling was not filled because of time constraints. West slope sampling did permit identifying the exact transition between *N. res* and *N. australis* (WA-1023). Similarly, the east slope of the South Ningbing Range (Map 23) shows a collecting gap of about 1 km along the limestone edge from WA-1018 to WA-226. This area is a sheer cliff face. It was walked on two occasions. Dead examples of *C. primum* were noted on the ground, but no "good rubble" was spotted that would permit collecting a series of live individuals. In contrast, stations WA-617 through WA-623 mark our zigzagging efforts to locate (successfully), the transition point between *C. primum* and *C. grossum.*

Area calculations were done by estimating the size of all limestone exposures from which the species has been recorded. A few arbitrary allocations had to be made. In the South Ningbing Range (Map 23), *Cristilabrum buryillum* and *C. simplex* are "credited" with the entire large mass south-southwest of Buryill Point, although records are only from its eastern face. The small hills to the northwest at the top of the map are, in contrast, ignored, as they have not yet been visited and we thus do not know what species lives there. Only the east edge of the large mass above Four Mile Creek (lower left of Map 23) has been included in the area estimate for *C. bubulum,* because this mass is a flat dome of unvegetated and unfissured rock that provides no snail aestivation sites. Including all of The Pillars (Map 21) as range for *Turgenitubulus aslini* is based on its presence at several stations, and the small distances between all rock masses in this part of the range.

More detailed collecting will alter some of the linear ranges by a few hundred meters at most, and may increase or decrease particular area estimates by up to 0.5 km^2 for some of the larger ranges. Any new species that are added undoubtedly will have ranges near the lower end of the distribution, since there are no large unsampled areas of good snail habitat left. Details of the range data will change, but the basic picture should remain the same.

The above comments provide necessary background to the discussion of actual ranges.

Table 4 lists the ranges in taxonomic order. The median inhabitable linear ranges within each genus are essentially identical, considering the small number of species and proportionately great range within genera. The smaller area ranges of *Cristilabrum* species probably reflect the fact that it occupies a smaller *total* area of limestone (see Maps 14, 20, 23, 25) than do the other genera. There is simply no *space* available for large area ranges. It is concluded that there is no *inherent* generic level difference in range pattern.

A distinction is made in Tables 4 and 6 between "linear range" and "habitable range". The former is the gross distance between extreme populations; the latter is the gross distance minus the areas of black mud or alluvial plains in which these camaenids cannot live. The four species in which there is a significant difference between linear and inhabited range (Table 6) all involve "small island" ranges. *Ningbingia bulla* is found on the north tip of the main mass of the North Ningbing Range (Map 17), but also lives on very small isolated hillocks scattered to the north (Maps 16, 17). These outlying colonies are near the banks of the unnamed creek (Map 14) that drains much of the east slope of the North Ningbing Range. Floods could easily transport examples of *N. bulla* washed off the main mass out to these northern isolates. *Turgenitubulus christenseni* (Maps 18-19) lives on both sides of Tanmurra Creek, partly on a peninsula, partly on isolated hillocks. *Cristilabrum isolatum* (Maps 22, 25) lives in the Sandy Creek area on two very small and isolated hills. *Cristilabrum spectaculum* (Maps 22, 25) is generally distributed through the scattered Jeremiah Hills. Given the present immature drainage of this area, flooding probably would accidentally transport both of these species from isolated hill to isolated hill.

The species are listed in order of linear habitable range in Table 5. Five species ranges are more than 4 km: three are *Ningbingia* from the very large mass of the North Ningbing Range (Maps 16-17); *Turgenitubulus aslini* (Maps 19, 21) lives in both The Gorge and The Pillars; and *Cristilabrum bubulum* (Maps 22-24) extends along the cliffed margin of a large dome formation.

The area occupied by each species is listed in ascending size in Table 7. Those with the five largest ranges, over 3 km², are almost the same group that showed the greatest linear ranges. The exception is the deletion of *Cristilabrum bubulum* (Maps 22-24), whose area is reduced in size because much of its range apparently is along a cliff face, and the substitution of *Turgenitubulus pagodula* (Maps 19, 21), which ranges throughout the large mass of The Gorge. The most extraordinary fact is that 20 (71.4%) of the species *each* have a total species range area of 1.2 km² or less.

The basic facts of distribution outlined above are simple. Explanation of the patterns is complicated. Much will have to be deferred to a subsequent discussion of phylogenetic patterns.

Certainly one facet of critical importance in understanding this distribution pattern is that all of the species show the same aestivation strategy and feeding structures. This undoubtedly reflects the fact that there is a defined wet season with more than 700 mm of annual rainfall (Table 1). Leaves and grass fragments are a plentiful source of food. The estimated 78 "snail activity nights" provide plenty of time for feeding. In the western Napier Range, where both the median annual rainfall (644 mm) and rain days (40) (Solem and Christensen, 1984: 473, Table 1) are somewhat less (compare Table 1), there is divergence in feeding structures and food resources where *Amplirhagada* Iredale, 1933 and *Westraltrachia* Iredale, 1933 become sympatric (Solem, 1985a). Rainfall data for Napier Downs station is incomplete, but in the 1979-1980 wet season, which had 667 mm total, therewere 18 rain events producing 66 SAN, compared with 12 events and 78 SAN at Carlton Hill. The limestone ridges at Napier Downs thus had more rain events, but a lowered total activity time. The differences, although small, may be enough to explain the feeding specializations found in the Napier Ranges. In the Cape Range, where mean annual rainfall is only 272.3 mm and there are 24.8 SAN scattered over eleven months, rather than concentrated in a wet season (see above), all five camaenid species show different radular structures (Solem, 1974: 152-155, figs 7a-f) that correlate with specialized food sources. They also show varied aestivation strategies and epiphragm structures, again contributing to minimizing competition during their brief times of activity.

The restricted range Ningbing camaenid species all have generalized radula and jaw structures. They all aestivate the same way — lying loose on the soil or rubble surface with a sheet of calcified mucus secreted across the shell aperture. The non-restricted range camaenid *Xanthomelon obliquirugosa* (E. A. Smith, 1894) is an exception to the latter, in that it apparently aestivates by burrowing into the ground and tends to have a mucoid, rather than a calcified epiphragm.

The restricted endemic Ningbing taxa show none of the above specializations. It is thus hypothesized that competition for food or aestivation site is not a factor in evolution of the Ningbing camaenids. The Mitchell Plateau *Amplirhagada* (see Solem, 1981a: 151, 275, 285, 292-293) have habitat specializations and aestivation differences, despite the more than doubled annual rainfall (Table 1). This serves to emphasize the complexity of speciation patterns in the Kimberley.

The pattern of generic distribution is simple. *Ningbingia* is restricted to the North Ningbing Range and a tiny southeast outlier (Maps 15-18). Less than 0.65 km separates the hill on which *Ningbingia australis elongata* lives and the first record of *Turgenitubulus christenseni* (Map 18). *Turgenitubulus* lives on isolated hills (Map 18) between the North and Central Ningbing Ranges, throughout most of the Central Ningbing Range, The Gorge, and The Pillars (Maps 19-22). In the southern part of the Central Ningbing Range (Maps 20, 22) there is an intrusion by *Cristilabrum rectum* and *C. solitudum,* separated from the main distribution of *Cristilabrum* by the range of *Turgenitubulus pagodula* and *T. aslini* in The Gorge and The Pillars (Map 22). The South Ningbing Range (Maps 23-24) and the Jeremiah Hill areas (Map 25) have most species of *Cristilabrum.* The only example of intergeneric sympatry involves *Cristilabrum* and the intrusion of *Ordtrachia elegans* into an eastern outlier of the Jeremiah Hills (WA-435, WA-987, Map 25). Nowhere are *Ningbingia, Turgenitubulus,* or *Cristilabrum* known to be microsympatric.

The patterns of species transitions are diverse, corresponding in part with the nature of the rock masses involved. *Ningbingia,* restricted to the North Ningbing Range (Maps 16-17), has a nearly continuous rock habitat, that, viewed from a helicopter, looks habitable throughout its extent. The major break in the rock mass, Utting Gap, is not a barrier to any species. Both *N. res* and *N. octava* have been found live on both sides of Utting Gap, and one dead example of *N. laurina* has been taken on the south side of the gap at WA-662 (Maps 16-17). The area north of Utting Gap and the fragmentary hillocks at the north tip have most of the species. Microsympatry is quite extensive in the area above No. 8 Bore (Table 8, Maps 16-17), with two species, *N. laurina* and *N. octava,* having been found only with other species — *laurina* with *dentiens, octava* and once with *res; octava* with either *laurina* or *res. N. dentiens* has less than 100 meters in which it occurs by itself (WA-981, Map 17), otherwise overlapping with *N. bulla* and *N. laurina.* Sympatry between *N. octava* and *N. res* starts well above Utting Gap, and reaches its southern side, but only *N. res* continues south. It is the only species present for perhaps a kilometer, and then is abruptly replaced by *N. australis australis* on the west face at WA-1023 and probably equally abruptly on the east face somewhere between WA-643 and WA-644 (Map 17). *N. a. australis* occupies the remainder of the North Ningbing Range and its outlying hills (Maps 17-18). An anatomically differentiated subspecies, *N. a. elongata,* lives on a small, isolated hill lying about 0.8 km southeast. At the north tip, *N. bulla* extends northwards on isolated limestone after its short overlap with *N. dentiens.*

Turgenitubulus, which mostly inhabits areas broken up into small to medium sized hills (Maps 18-22), shows much less sympatry (Table 8). Both *T. pagodula* and *T. aslini* occupy the mass of The Gorge, which, like the North Ningbing Range, shows near continuous vegetation viewed from a helicopter and thus is considered to be good snail habitat. Only *T. aslini* extends southeast into The Pillars (Maps 19, 21), and it also has been collected alone on northeast (WA-1028, Map 21) and west faces (WA-1004, Map 21) of The Gorge. More detailed collecting in The Gorge region is needed. *T. depressus* (Maps 19-20) occupies a very small area in sympatry with *T. opiranus.* The former has been found alone (WA-1044b) "under figs on top of saddle just north of peak", but otherwise always with examples of *T. opiranus* in the area of overlap. The latter extends both north and south of the overlap area (Map 19).

The other *Turgenitubulus* species show abrupt transitions (Maps 18-20), either *along* a rock mass (*christenseni-opiranus,* possibly *costus-tanmurranus*) or *on either side of* a gap between rock masses (*opiranus-foramenus, foramenus-costus,* possibly *costus-tanmurranus*). The break between *T. tanmurranus* and *Cristilabrum solitudum* (Maps 20, 22) occurs on either side of a gap between rock masses.

The northern outliers of *Cristilabrum* in the Central Ningbing Ranges (Maps 20, 22), *C. solitudum* and *C. rectum,* occupy different sets of limestone islands, based on still limited collecting.

In the Jeremiah Hills and outliers (Map 25), *Cristilabrum isolatum* lives on northwest isolated limestone hills, *C. spectaculum* is generally distributed in the Jeremiah Hills and eastern outliers, with one sympatric record to the east, where it has been found with *C. bilarnium* and the one intrusion of *Ordtrachia* into the region.

In the main masses of the SouthNingbing Ranges (Maps 23-24), *C. simplex* and *C. buryillum* only have been found together on several sets of hills. There is then a gap of uninhabitable plains to the range of *C. monodon,* found along a large mass, on a small outlying hill, and then on the north tip of the main mass (WA-607, WA-1015). *Cristilabrum* probably new species is found on isolated hills to the west. On the main mass, there are abrupt "same mass" transitions from *monodon* to *primum* to *grossum*, which occur in a few meters. The two species will be found in rubble piles on opposite sides of a very small cliff or valley. The next transition, from *C. grossum* to *C. bubulum*, occurs across a plains gap of less than 75 meters.

To summarize the above, species transitions in the North Ningbing Ranges normally involve a zone of sympatry (Table 8); in contrast, sympatric occurrences are rare in both *Turgenitubulus* and *Cristilabrum* (Table 8). The pattern of species whose boundaries do not include a zone of sympatry, can be divided into three categories, the last two of which are somewhat arbitrary in their separation: 1) abrupt shift along a continuous rock mass; 2) abrupt shift across a narrow gap of plains; and 3) species found on well isolated limestone masses. These are:

Abrupt shift on same mass
- *Ningbingia res-N. australis australis*
- *Turgenitubulus christenseni-T. opiranus*
- *?Turgenitubulus costus-T. tanmurranus*
- *Cristilabrum monodon-C. primum*
- *C. primum-C. grossum*

Shift across narrow gap
- *Ningbingia a. elongata-Turgenitubulus christenseni*
- *T. opiranus-T. foramenus*
- *?T. costus-T. tanmurranus*
- *T. tanmurranus-Cristilabrum solitudum*
- *C. solitudum-C. rectum*
- *C. rectum-T. aslini*
- *C. simplex* and *C. buryillum-C. monodon*
- *C. grossum-C. bubulum*

Shift across wider gap
- *Ningbingia a. australis-N. a. elongata*
- *Cristilabrum monodon-C.* probably new species
- *C. isolatum-C. spectaculum*

Of all the above species transitions, only one, that between *Ningbingia res* and *N. australis*, shows any indication of possible hybridization or introgression. The lip knob and body whorl sulcus that are characteristic of *N. res* (Solem, 1981b: 340, figs 78b, d) become greatly reduced to lost at WA-643, WA-1023a, and WA-1023b (Map 18), the stations just before collections of *N. a. australis* at WA-1023c and WA-644. Available genital anatomies do not show evidence of intergradation in these populations. More detailed discussion of this will be given elsewhere.

The abruptness of the species transitions along continuous cliffs is surprising. In every situation that we have pinpointed, the transition is sudden and absolute. There are no situations in which there is a mosaic of alternating populations, only a complete change from one species to the next.

Equally interesting, there is only one species, *Ningbingia laurina*, which appears to be actually rare and possibly with a constricting range. Only nine live examples were collected, compared with 109 dead examples (8.2%), and these were found in the central portion of the species range, from WA-997 (ca 1.5 km northwest of No. 8 Bore) south to WA-434 (ca 0.75 km southwest of No. 8 Bore) (Map 17). No live *laurina* were found in the overlap areas with either *dentiens* or *res*, but live examples of both *laurina* and *octava* were taken microsympatrically.

The species pairs that do have overlap zones (Table 8) agree in that the ranges of both species are continuous throughout the overlap area. At a few stations, collecting effort yielded less than five shells of only one species, thus creating an almost certainly artificial gap in the range. These situations have been ignored. The nature of the overlap zones varies. *Turgenitubulus depressus* is a short range species encompassed within a much larger range; *Ningbingia laurina, N. octava*, and *N. res* have individually large ranges that variously overlap; *T. aslini* shares an extensive range with *T. pagodula*, and then extends into a second major area; *Cristilabrum simplex* and *C. buryillum* have ONLY been collected sympatrically; the northern *Ningbingia* show simple overlap; and the Jeremiah Hill taxa show two restricted range species, *Cristilabrum bilarnium* and *Ordtrachia elegans*, which are joined by a more widely distributed species, *C. spectaculum*.

Most of the overlap zones are small, occupying less than 0.33 km^2. Four pairs (Table 8) have an area of sympatry that is more than 1 km^2. It is not sufficient merely to list these zones. The question as to whether they reflect a static situation, or might indicate dynamic change, can be addressed in a preliminary fashion. It must be emphasized that collecting time at individual stations varied greatly, hence the number of specimens collected is not indicative of actual abundance at different stations. While an attempt was made to take all adult examples exposed by rock moving at a particular station, there is a natural tendency to pick up a "rarer" species that probably biased the numbers at some stations. Despite the above, the numbers of specimens collected are the only evidence we have available. The numbers and proportions of the species that have been collected within the zones of sympatry are summarized in Tables 9-10, separated into live and dead adults.

Interpretation of Table 9 requires the additional cautionary comment that *Ningbingia laurina* always is a rare species. Thus its minor representation in areas of sympatry with *N. dentiens* and *N. octava* may have no significance. In contrast, the proportions of *N. bulla* and *N. dentiens* may indicate that actual replacement of the former is occurring. Few of the dead *N. bulla* from WA-634 and WA-704 were "fresh", but some of these may have been dead for only one or two years. It is not possible to use available specimens to predict that *N. bulla* is extinct in this zone, but that species may be greatly reduced in numbers.

The remaining summary numbers (Table 9) suggest primarily that more field work is needed. The relative numbers of live compared with dead adults vary substantially within each pair — except for the Jeremiah Hills *Cristilabrum bilarnium-C. spectaculum.* The term substantially, rather then significantly, is used deliberately. Neither quadrats nor "collecting time" standards were used in the collecting, and it must be reemphasized that specimens are clustered, rather than randomly distributed. Hence I did not consider the summary numbers precisely comparable and thus suitable for statistical analysis. Nevertheless, they do suggest that differences occur and further field study is warranted.

For the three species that have larger areas of sympatry and do not involve the rare species, *Ningbingia laurina*, the numbers for individual stations are presented in Table 10.

Ningbingia res and *N. octava* are microsympatric along the east slope from WA-664, 1.1 km north of Utting Gap, to the southeast margin of Utting Gap (WA-662). They also have been collected together at the west entrance to Utting Gap (WA-996). The considerable differences in numbers and proportions of dead adults suggest that there may be actual differential abundance, but there is no linear geographic pattern to these changes. The numbers of live adults are small enough at most stations to prevent any meaningful statement.

In the mass of The Gorge (Map 21), clearly there are shifts in relative abundance of *T. pagodula* and *T. aslini.* WA-1029 is on the northern margin of the mass; WA-646 and WA-648 are on the north side of Station Creek; WA-649-50 on the south side of Station Creek; and WA-1030 is at the tip of the southeast peninsula from The Gorge. Not only are there differences in proportions of species from station to station, but there is a difference from collecting visit to collecting visit. In 1980, L. Price and F. Aslin collected 23 live adult *T. pagodula* and 6 live adult *T. aslini* from WA-646, a small gully. This was the largest number of the former species collected that year. Thus, in 1984 we returned to this station (numbered WA-1039 in 1984) to collect material for electrophoretic studies, but obtained only one live and one dead adult *T. pagodula* — despite L. Price taking us into the identical small gully. The reasons for the differential abundance remain to be discovered.

Finally, *Cristilabrum simplex* and *C. buryillum* have congruent ranges, but show a geographic change in relative abundance (Table 10). They occupy a line of hills running southeast and south-southeast of Ningbing Bore (Map 23). On the northernmost hill (WA-669, WA-1019), *N. buryillum* clearly is dominant in live adults, but the situation reverses for dead adults; on one sampled part of the central, very large hill (WA-235, WA-602), the same pattern exists, but slightly further south

(WA-671) the dominance of *N. simplex* includes both live and dead examples; on the small southern hill (WA-670), only a few dead *N. buryillum* were obtained, but many live and dead *C. simplex*. The stations all have the same eastern exposure. I have no explanation for the change in species numbers, but this is another situation requiring field investigations.

In summary, while most species are allopatric, the varied patterns of sympatry that do exist provide opportunities for field investigations of possible species replacement phenomena and interactions. The existence of the overlap zones has been documented. The dynamics and significance of these zones need to be studied.

IMPLICATIONS FOR CONSERVATION BIOLOGY

The accelerating rate of extinction through massive destruction of habitats has created a crisis situation, especially in regard to the terrestrial tropics. The dual concepts of salvage collecting and creating reserves that will enable survival of at least some tropical diversity are driving the efforts of research biologists and conservationists.

Most effort to date has been focused on the large, conspicuous organisms, plants and vertebrates, whose taxonomy and distributions are much better known than those of the invertebrates. A new discipline of "Conservation Biology" has emerged as a leader in these efforts (Soulé, 1986). Its proponents are critically examining such factors as "Minimum Viable Population Size" and needed "Reserve Areas". With the focus on vertebrates, a coarser grain approach to area needs is being taken. Terborgh and Winter (1983), for example, utilized a range of less than 50,000 km^2 as indicative of local endemism in bird faunas, pointing out that 440 South American species (about one-quarter) met this criteria, but only eight North American bird species were similarly restricted. Gentry (1986) also accepted defining "local endemic plants" as those with ranges of 50,000 km^2 or less, but also recorded several taxa with much smaller ranges.

Land snails require a finer grained approach. The Ningbing Ranges-Jeremiah Hills radiation of 28 camaenid land snails occurs within a total area of about 115 km^2. The Ningbing Ranges and connecting plains occupy about 85 km^2, and the much smaller limestone masses of the Jeremiah Hills are scattered over some 30.5 km^2. The individual species have a median range of 0.825 km^2 and a median linear range of 1.65 km. This entire radiation occupies about 0.23% of the 50,000 km^2 that defines a "localized range" vertebrate or plant species. These snails do not, and will not, have the public recognition or appeal of a panda, a whooping crane, or perhaps even a lousewort. They can, however, serve to identify unique biological areas, worthy of conservation, and salvable at exceedingly modest costs compared with the needs of the better publicized taxa.

The Ningbing Range story points out how spectacular evolutionary radiations can occur in minimal areas without significant sympatry among the taxa. Earlier work of Solem, Climo and Roscoe (1981) and Solem and Climo (1985) demonstrated that in mid-North Island, New Zealand, more than 70 species of land snails can be micro-sympatric and survive in very small patches of gully vegetation.

It is hoped that such studies can be combined with work on the terrestrial arthropods to identify, publicize, and preserve at least a portion of such microcosms before they go the way of most Pacific Island organisms — extinction (Solem, In press — B).

Small areas are not insignificant to conservation of evolutionary diversity — only not recognized and promoted as being worthy of attention.

DISCUSSION AND CONCLUSIONS

The above review has attempted to develop or summarize several aspects of the Ningbing Ranges-Jeremiah Hills land snail fauna. The discussion of moisture availability and its translation into *snail activity nights* (SAN) represents a new approach to land snail distribution and ecology that can be applied to many other areas of the world. While it will be modified in detail, the demonstration that desert and semi-arid area land snails must compress activity into very short periods and during only a fraction of the year, has fundamental implications in understanding their ecology.

The land snail fauna of the Ningbing Ranges and Jeremiah Hills is of mixed significance. Presently published data on land snail distribution within Australia is inadequate to make major area comparisons. The most recent summary (Bishop, 1981) lists previous contributions and then discusses general philosophical problems of systematics and biogeography as not even family presence or absence in many parts of Australia had been recorded.

There are three parts to the Ningbing land snail fauna: 1) indigenous species which have extensive extralimital ranges (13 species); 2) restricted endemic species found throughout the Ningbing Ranges, whose few Australian relatives are far away (*Georissa, Gyliotrachela ningbingia*); and 3) short range endemic camaenids occupying basically allopatric ranges within short sections of the Ningbing Ranges or Jeremiah Hills (28 species).

The more widely distributed taxa are dry country dwellers within the main ranges, plus a few wetter area taxa on the margins of Brolga Spring, the only permanent body of water. The rain forest areas in the Northern Territory from Melville Island south to the Roper River, and in the Kimberley from Yampi Sound northeast to the Drysdale River, share a number of land snail species that currently are absent from the Ningbing area. Presumably they would have been present in wetter eras. Whether the current main mass dry country snails are colonizers from the south, persistant long term residents, or a combination, is unknown, and probably unimportant. The wet area taxa from near Brolga Spring could be relicts, or, more probably, recent colonizers brought in accidentally by water fowl. They all have the "sticky mucus" characteristic of "bird hitching" snails.

Enough collecting has been done in the Northern Territory by Vince Kessner in recent years, and in the Kimberley during the course of my own research, to indicate that the restriction of *Georissa* to Queensland-New South Wales and the Ningbing Ranges seems genuine, as is the Napier Range-Ningbing Range-Katherine northern Queensland range of *Gyliotrachela*. They are notable records biogeographically.

While *Ordtrachia elegans* is a member of a genus of the East Kimberley that is found as far south as Nicholson, the other three genera, *Ningbingia, Turgenitubulus, Cristilabrum*, with 27 known species are found only in this area. *Ningbingia* may be most closely related to *Prymnbriareus* from the Salmond-Pentecost-Chamberlain River area, while *Turgenitubulus* is descended from *Cristilabrum*. Both of the latter genera are very different from *Ningbingia* and may find their closest relative in *Mesodontrachia* from the Cockburn Range southwest of Wyndham and into the Northern Territory.

The phyletic relationships of the genera will be discussed elsewhere. Here it is important to note that the Ningbing genera are restricted endemics. Diversification has occurred *in situ* within the Ningbing Ranges and Jeremiah Hills, filling the available limestone exposures with short range taxa that show no indication of specialization in feeding or aestivation strategy, aspects of camaenid land snail life that show significant local specialization in other dry areas of central and Western Australia.

The basic pattern of range size and transitions has been outlined, and introductory notes concerning the zones of sympatry presented to encourage additional field work. Most species show considerable shell variation among local populations. Discussion of these patterns, electrophoretic data, anatomical trends, and a hypothesis of speciation events will be developed subsequently. The data simply are too massive to include within this report, which is to be viewed as a summary of distributional facts, thus background to more theoretical discussions.

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TABLE 1. Rainfall and wet season length patterns, selected stations

	Rain Gauging Station							
	Mitchell Plateau	Kalumburu	Carlton Hill	Ivanhoe	Kimberley Research	Kununurra	Lissadell	Halls Creek
Location	14° 49′ 125° 50′	14° 16′ 126° 36′	15° 29′ 128° 32′	15° 42′ 128° 41′	15° 39′ 128° 42′	15° 47′ 128° 44′	16° 40′ 128° 33′	18° 14′ 127° 40′
1951-1976								
Annual Rainfall in mm								
MEAN & RANGE	1593	RECORDS	776[1] (398-1442)	802[2] (380-1441)	NOT IN	NOT IN	589	491
MEDIAN	1563	INCOMPLETE	732[1]	726[2]	EXISTENCE	EXISTENCE	581	497
Total Rain Days								
MEAN & RANGE	97		45[1] (35-65)	47[1] (30-62)			37	60
1974-1984								
Annual Rainfall in mm								
MEAN & RANGE	1548 (1233-1904)	1154 (728-1566)	RECORDS ARE		794[3] (591-1088)	842 (646-1178)	673 (394-870)	655 (357-992)
MEDIAN	1508	1273	INCOMPLETE		758[3]	797	686	632
Total Rain Days								
MEAN & RANGE	100 (86-118)	86 (68-116)			77[3] (67-103)	69 (55-90)	39 (29-44)	67 (44-99)
Wet Season Length								
First Rain								
MEAN & RANGE	17 Oct (18 Sep-4 Dec)	25 Oct (20 Sep-20 Nov)	5 Nov[1] (9 Oct-1 Dec)	1 Nov[2] (1 Oct-16 Nov)	24 Oct[3] (1 Oct-20 Nov)	22 Oct (18 Sep-20 Nov)	1 Nov (6 Sep-12 Dec)	3 Oct (7 Sep-8 Dec)
Second Rain								
MEAN & RANGE	5 Nov (4 Oct-8 Dec)	13 Nov (30 Sep-9 Dec)	30 Nov[1] (20 Nov-31 Dec)	20 Nov[2] (9 Oct-25 Dec)	13 Nov[3] (20 Oct-8 Dec)	8 Nov (28 Sep-7 Dec)	20 Nov (6 Oct-27 Dec)	26 Nov (1 Oct-3 Jan)
MEAN & RANGE OF GAP	18.5 (4-35)	19.4 (5-43)	15.8[1] (8-36)	18.8[2] (7-41)	18.0[3] (3-38)	16.5 (8-30)	18.5 (7-43)	26.9 (5-111)
Next to Last								
MEAN & RANGE	30 Mar (16 Mar-1 May)	2 Apr (15 Mar-14 May)	26 Mar[1] (23 Feb-22 May)	29 Mar[2] (28 Feb-21 May)	19 Mar[3] (11 Feb-2 Apr)	23 Mar (11 Feb-16 May)	3 Mar (10 Feb-2 Apr)	25 Mar (13 Feb-17 May)
Last Rain								
MEAN & RANGE	20 Apr (31 Mar-25 May)	18 Apr (24 Mar-26 May)	5 Apr[1] (8 Mar-26 May)	14 Apr[2] (6 Mar-26 May)	7 Apr[3] (1 Mar-24 May)	6 Apr (18 Feb-24 May)	23 Mar (17 Feb-10 May)	5 Apr (17 Feb-27 May)
MEAN & RANGE OF GAP	19.4 (3-70)	16.5 (4-36)	10.4[1] (4-25)	15.6[2] (4-39)	19.4[3] (2-59)	18.7 (4-60)	19.2 (6-68)	12.3 (4-21)
Average Length:								
1st to Last	185 days	175 days	151 days	164 days	165 days	165 days	143 days	183 days
2nd to Next to Last	154 days	140 days	116 days	129 days	126 days	135 days	103 days	119 days

[1] — only 7 years; [2] — only 8 years; [3] — only 10 years.

TABLE 2. Endemic land snails, except restricted range species

- **Subclass Prosobranchia**
  - Order Diotocardia (=Archaeogastropoda)
    - FAMILY HYDROCENIDAE
      - **Georissa* new species[1]
- **Subclass Pulmonata**
  - Superorder Stylommatophora
    - Order Orthurethra
      - FAMILY PUPILLIDAE
        - *Pupisoma orcula* (Benson, 1850)
        - *Pupisoma* sp.
        - *Nesopupa mooreana* (E. A. Smith, 1894)
        - *Gastrocopta* new species[1]
        - **Gyliotrachela ningbingia* Solem, 1981
        - *Pupoides pacificus* (Pfeiffer, 1846)
    - Order Sigmurethra
      - Suborder Holopodopes
        - FAMILY SUBULINIDAE
          - *Eremopeas interioris* (Tate, 1894)
      - Suborder Aulacopoda
        - FAMILY HELICODISCIDAE
          - *Stenopylis coarctata* (Moellendorff, 1894)
        - FAMILY CHAROPIDAE
          - *Discocharopa aperta* (Moellendorff, 1888)
        - FAMILY SUCCINEIDAE
          - *Austrosuccinea* (= *Succinea*) sp.
        - FAMILY HELICARIONIDAE
          - *Coneuplecta (Sitalina) microconus* (Mousson, 1865)
          - *Westracystis lissus* (E. A. Smith, 1894)
      - Suborder Holopoda
        - FAMILY CAMAENIDAE
          - *Xanthomelon obliquirugosa* (E. A. Smith, 1894)
          - *Torresitrachia weaberana* Solem, 1979

[1] — These species are being described by Solem (In press — A)

* — Indicates species restricted to the Ningbing-Jeremiah area

TABLE 3. Composition of restricted range camaenid radiation

Genus	Number of species	Range
Ningbingia Solem, 1981	6[1]	N Ningbing Range
Turgenitubulus Solem, 1981	8	Central Ningbing Range, The Gorge, The Pillars
Cristilabrum Solem, 1981	12	S tip Central Ningbing Range, S Ningbing Range, Jeremiah Hills, E outliers
Ordtrachia Solem, 1984	1[2]	E outliers of Jeremiah Hills, both sides of Lake Argyle S to Nicholson River

[1] — Plus one named subspecies

[2] — Plus four named and additional unnamed extralimital taxa

TABLE 4. Restricted range land snails

Species	Linear range in km	Total Range: Habitable range in km	Area of range in km^2
FAMILY CAMAENIDAE			
Ningbingia			
bulla Solem, 1981	3.9	1.7	0.74
dentiens Solem, 1985	1.0	1.0	0.38
laurina Solem, 1981	5.0	5.0	3.95
octava Solem, 1981	4.5	4.5	5.60
res Solem, 1981	4.1	4.1	4.40
australis australis Solem, 1981	1.0	1.0	1.05
australis elongata Solem, 1988	0.1	0.1	0.01
MEDIAN and RANGE		1.7	1.05
		(0.1-5.0)	(0.01-5.60)
Turgenitubulus			
christenseni Solem, 1981	2.9	1.0	0.65
opiranus Solem, 1981	3.1	3.1	2.65
depressus Solem, 1981	0.2	0.2	0.26
foramenus Solem, 1981[1]	1.15	1.15	0.75
costus Solem, 1981[1]	1.8	1.8	2.20
tanmurranus Solem, 1985	2.0	2.0	1.13
pagodula Solem, 1985[2]	2.7	2.7	3.75
aslini Solem, 1985[2]	6.1	6.1	7.45
MEDIAN and RANGE		1.9	1.66
		(0.2-6.1)	(0.26-7.45)
Cristilabrum			
solitudum Solem, 1981	2.9	2.9	1.70
rectum Solem, 1988	1.2	1.2	0.29
simplex Solem, 1981	2.7	2.7	1.02
buryillum Solem, 1981	2.7	2.7	1.02
monodon Solem, 1985	0.9	0.9	0.61
new species	0.5	0.5	0.30
primum Solem, 1981	1.2	1.2	0.90
grossum Solem, 1981	0.5	0.5	0.31
bubulum Solem, 1981	5.0	5.0	0.66
bilarnium Solem, 1981	0.7	0.7	0.32
isolatum Solem, 1985	5.3	0.6	0.15
spectaculum Solem, 1985	8.3	1.6	1.20
MEDIAN and RANGE		1.4	0.63
		(0.5-5.0)	(0.15-1.70)
Ordtrachia			
elegans Solem, 1988	0.7	0.7	0.32

[1] — An unsampled mass of 0.52 km^2 probably contains one of these two species

[2] — Much of their range is interrupted by short gaps; most of the exposed limestone consists of solid masses that would not provide any shelter sites; thus calculation of their "occupied range" is very difficult and more than arbitrary.

TABLE 5. Restricted range species, linear habitable ranges in km.

N. australis elongata	0.1
T. depressus	0.2
C. rectum	0.5
C. grossum	0.5
C. isolatum	0.6
O. elegans	0.7
C. bilarnium	0.7
C. monodon	0.9
N. dentiens	1.0
N. australis australis	1.0
T. christenseni	1.0
T. foramenus	1.15
C. new species	*1.2*
C. primum	*1.2*
C. spectaculum	1.6
N. bulla	1.7
T. costus	1.8
T. tanmurranus	2.0
T. pagodula	2.7
C. simplex	2.7
C. buryillum	2.7
C. solitudum	2.9
T. opiranus	3.1
N. res	4.1
N. octava	4.5
C. bubulum	5.0
N. laurina	5.0
T. aslini	6.1

MEDIAN RANGE = 1.65 km

TABLE 6. Restricted range species, linear vs habitable ranges in km

Species	Linear range	Habitable range
Ningbingia bulla	3.9	1.7
Turgenitubulus christenseni	2.9	1.0
Cristilabrum isolatum	5.3	0.6
Cristilabrum spectaculum	8.3	1.6

TABLE 7. Restricted range species, area of range in km²

N. australis elongata	0.01
C. isolatum	0.15
T. depressus	0.26
C. rectum	0.29
C. new species	0.30
C. grossum	0.31
C. bilarnium	0.32
O. elegans	0.32
N. dentiens	0.38
C. monodon	0.61
T. christenseni	0.65
C. bubulum	0.66
T. bulla	0.74
T. foramenus	0.75
C. primum	0.90
C. simplex	1.02
C. buryillum	1.02
N. a. australis	1.05
T. tanmurranus	1.13
C. spectaculum	1.20
C. solitudum	1.70
T. costus	2.20
T. opiranus	2.65
T. pagodula	3.75
N. laurina	3.95
N. res	4.40
N. octava	5.60
T. aslini	7.45

MEDIAN RANGE AREA = 0.825 km²

TABLE 8. Patterns of sympatry in restricted range endemics

Sympatric taxa	Total range in km²	Sympatric area in km²	% of total range
Ningbingia bulla	0.74	0.11	15%
N. dentiens	0.38	0.11	29%
N. dentiens	0.38	0.18	47%
N. laurina	3.95	0.18	4.5%

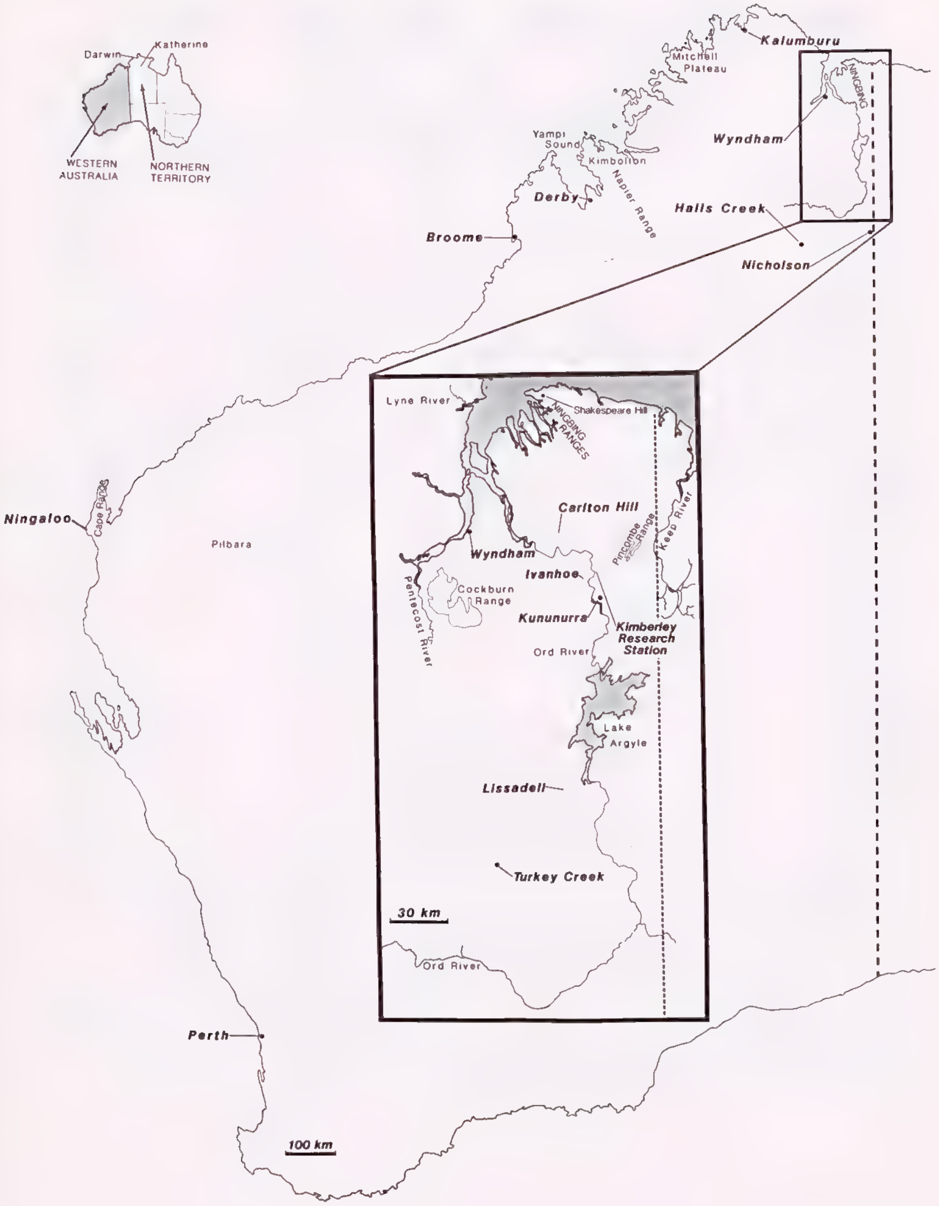
Sympatric taxa	Total range in km²	Sympatric area in km²	% of total range
N. laurina	3.95	3.78	96%
N. octava	5.60	3.78	68%
N. octava	5.60	1.83	33%
N. res	4.40	1.83	42%
Turgenitubulus depressus	0.26	0.26	100%
T. opiranus	2.65	0.26	10%
T. aslini	7.45	3.75	50%
T. pagodula	3.75	3.75	100%
Cristilabrum buryillum	1.02	1.02	100%
C. simplex	1.02	1.02	100%
C. bilarnium	0.32	0.32	100%
C. spectaculum	1.20	0.32	27%
Ordtrachia elegans	0.32	0.32	100%

TABLE 9. Species proportions within zones of sympatry

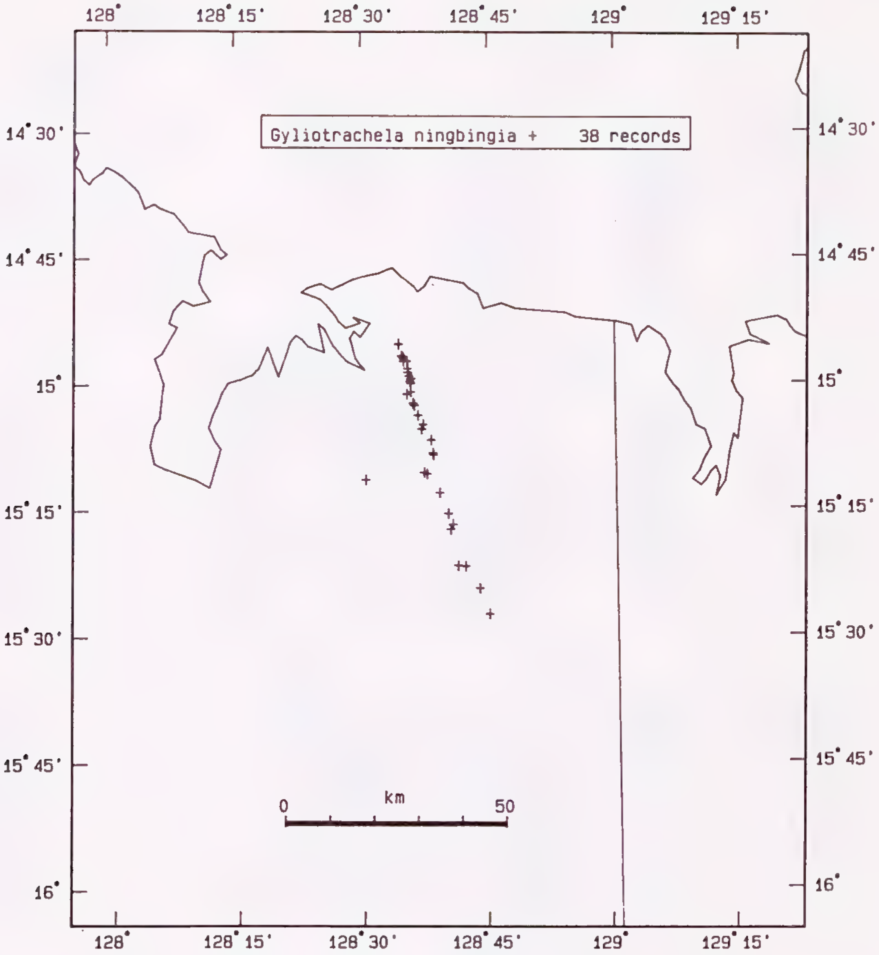
Species	Stations	Live adults	Dead adults
Ningbingia bulla	704, 634	0	68 (17%)
N. dentiens	704, 634	17 (100%)	333 (83%)
N. dentiens	700-701	82 (100%)	208 (87%)
N. laurina	700-701	0	30 (13%)
N. laurina	606-7, 997, 636	3 (3%)	46 (14%)
N. octava	606-7, 997, 636	87 (97%)	285 (86%)
N. octava	662-4, 640-1, 996	36 (32%)	443 (56%)
N. res	662-4, 640-1, 996	76 (68%)	381 (44%)
Turgenitubulus			
opiranus	227, 654, 1044	47 (76%)	514 (59%)
depressus	227, 654, 1044	15 (24%)	361 (41%)
pagodula	646-650, 1029-30	43 (44%)	200 (33%)
aslini	646-650, 1029-30	54 (56%)	401 (67%)
Cristilabrum			
simplex	235, 602, 669-71, 1019	56 (46%)	640 (82%)
buryillum	Same stations	66 (54%)	142 (18%)
bilarnium	435, 987	18 (53%)	203 (59%)
spectaculum	435, 987	10 (29%)	111 (32%)
Ordtrachia elegans	987	6 (18%)	33 (9%)

TABLE 10. Species proportions at individual stations where sympatric zones are large

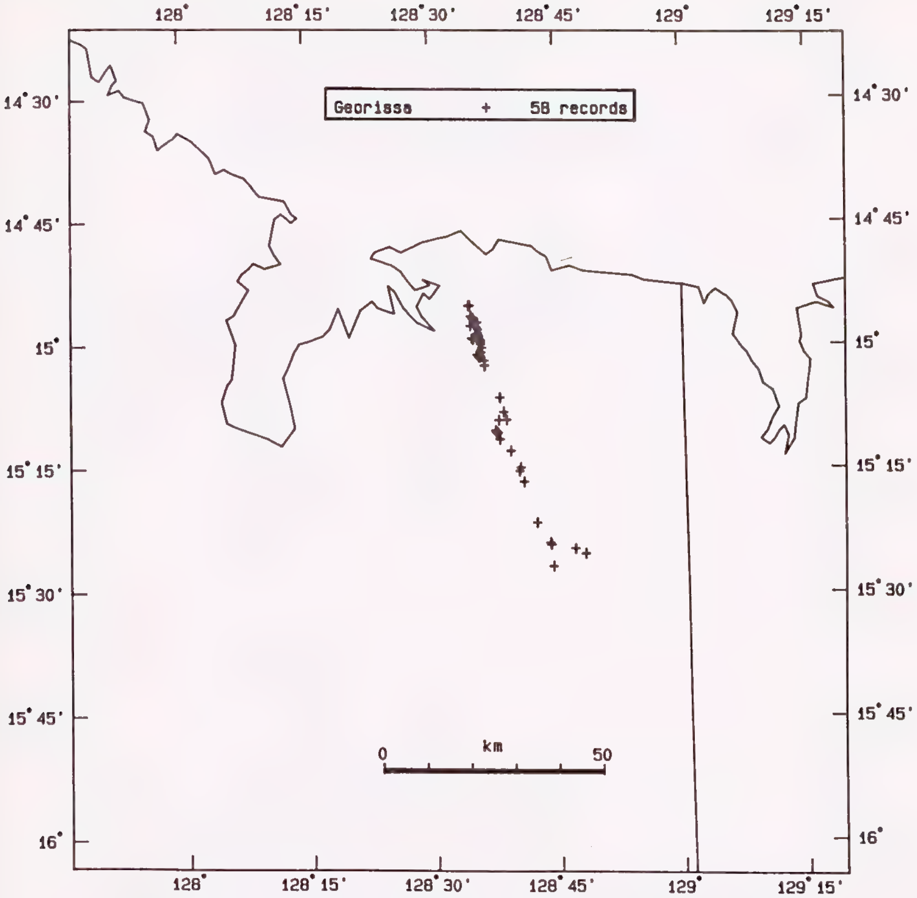
	Ningbingia			
	octava		*res*	
Station	Live	Dead	Live	Dead
WA-664	2 (67%)	109 (93%)	1 (33%)	8 (7%)
WA-663	15 (54%)	196 (87%)	13 (46%)	29 (13%)
WA-996	0 —	11 (17%)	14 (100%)	55 (83%)
WA-640	2 (25%)	34 (44%)	6 (75%)	43 (56%)
WA-641	16 (64%)	49 (75%)	9 (36%)	16 (25%)
WA-662	1 (3%)	44 (19%)	33 (97%)	230 (81%)
TOTALS	36 (32%)	443 (54%)	76 (68%)	381 (46%)
	Turgenitubulus			
	aslini		*pagodula*	
WA-1029	21 (91%)	32 (97%)	2 (9%)	1 (3%)
WA-648	4 (40%)	76 (71%)	6 (60%)	31 (29%)
WA-649	7 (64%)	106 (100%)	4 (46%)	0 —
WA-650	8 (80%)	24 (62%)	2 (20%)	15 (38%)
WA-646	6 (21%)	110 (54%)	23 (79%)	92 (46%)
WA-647	0 —	33 (40%)	6 (100%)	49 (60%)
WA-1030	8 (100%)	20 (61%)	0 —	13 (39%)
TOTALS	54 (56%)	401 (67%)	43 (44%)	200 (33%)
	Cristilabrum			
	simplex		*buryillum*	
WA-1019	10 (34%)	18 (62%)	19 (66%)	11 (38%)
WA-669	6 (29%)	138 (83%)	15 (71%)	29 (17%)
WA-602	13 (33%)	256 (76%)	27 (67%)	80 (24%)
WA-235	1 (100%)	93 (93%)	0 —	7 (7%)
WA-671	18 (78%)	29 (85%)	5 (22%)	5 (15%)
WA-670	8 (100%)	106 (91%)	0 —	10 (9%)
TOTALS	56 (46%)	640 (82%)	66 (54%)	142 (18%)



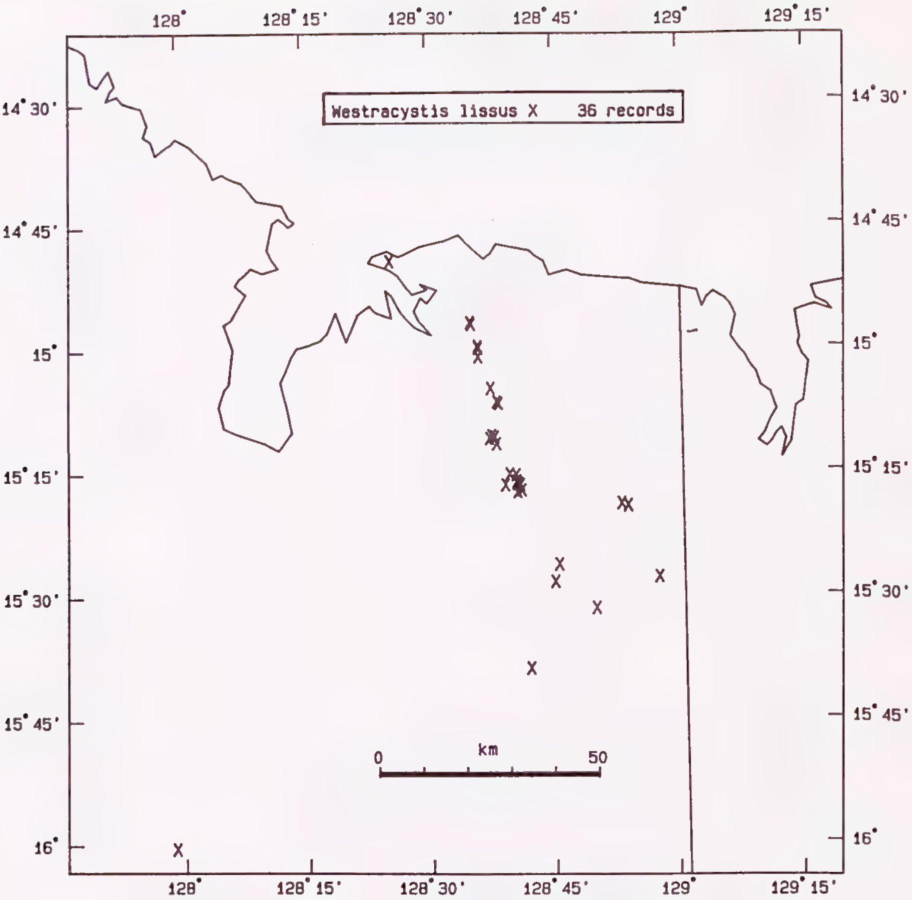
1. Location of the Ningbing Ranges and other mentioned localities in Western Australia.



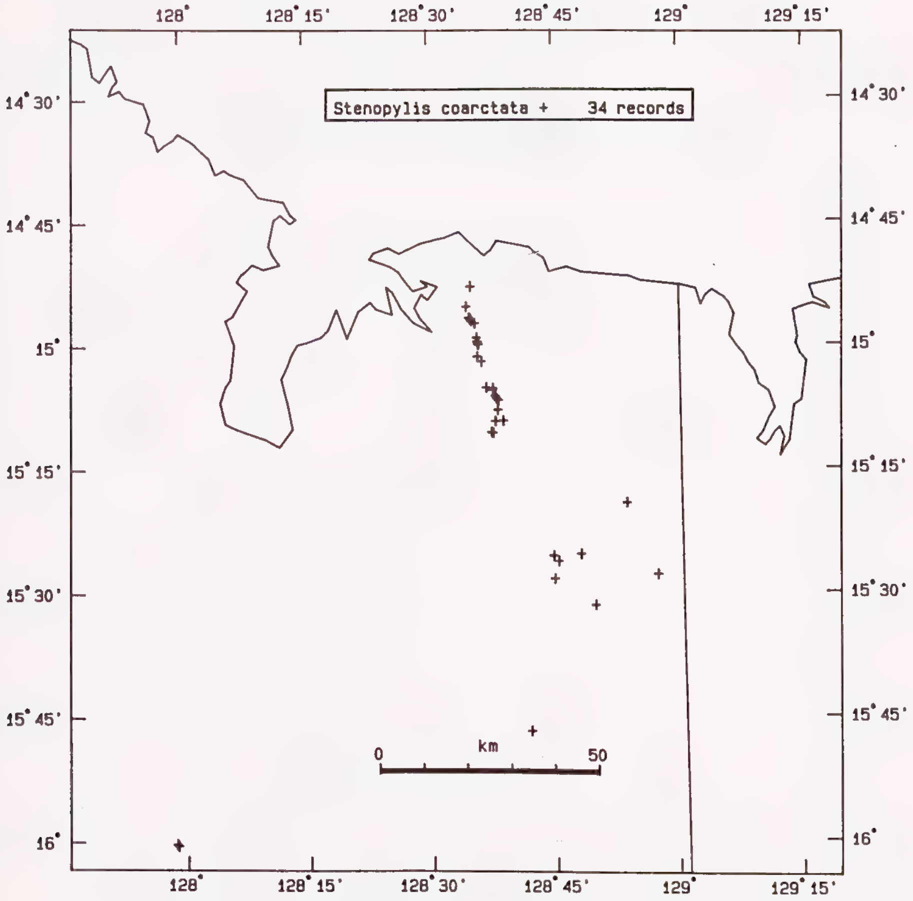
2. Distribution records of the restricted endemic species *Gyliotrachela ningbingia* Solem, 1981.



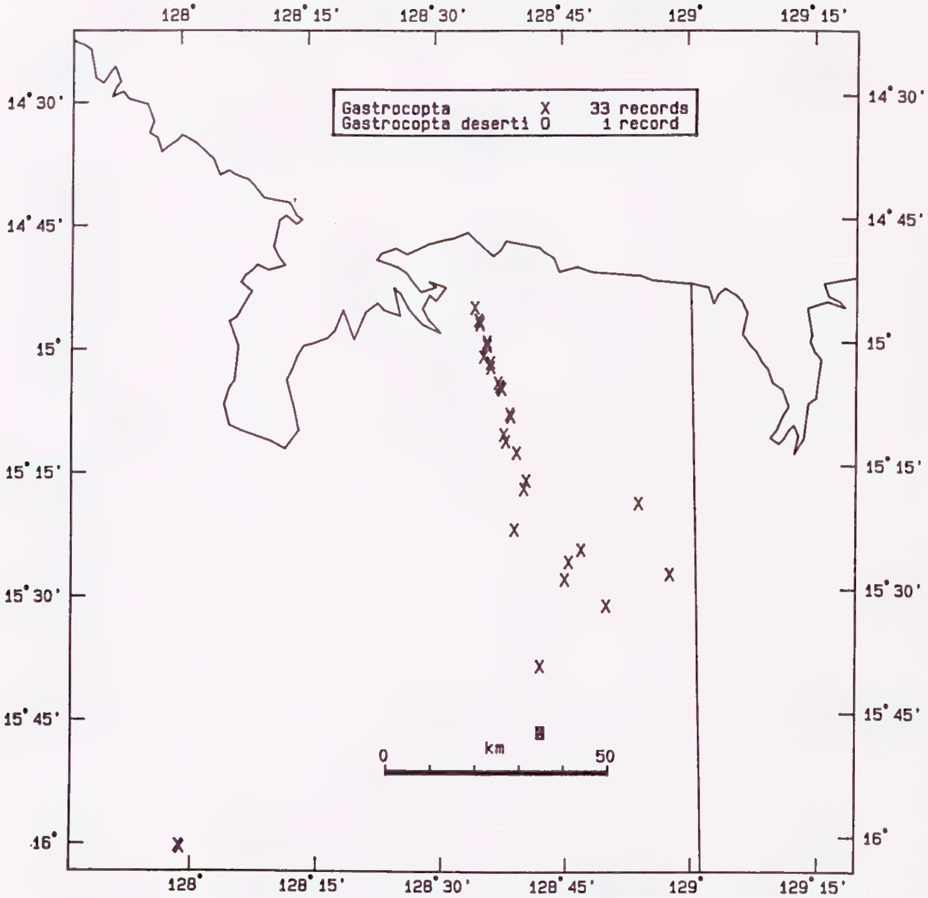
3. Distribution records of the restricted endemic species *Georissa* new species.



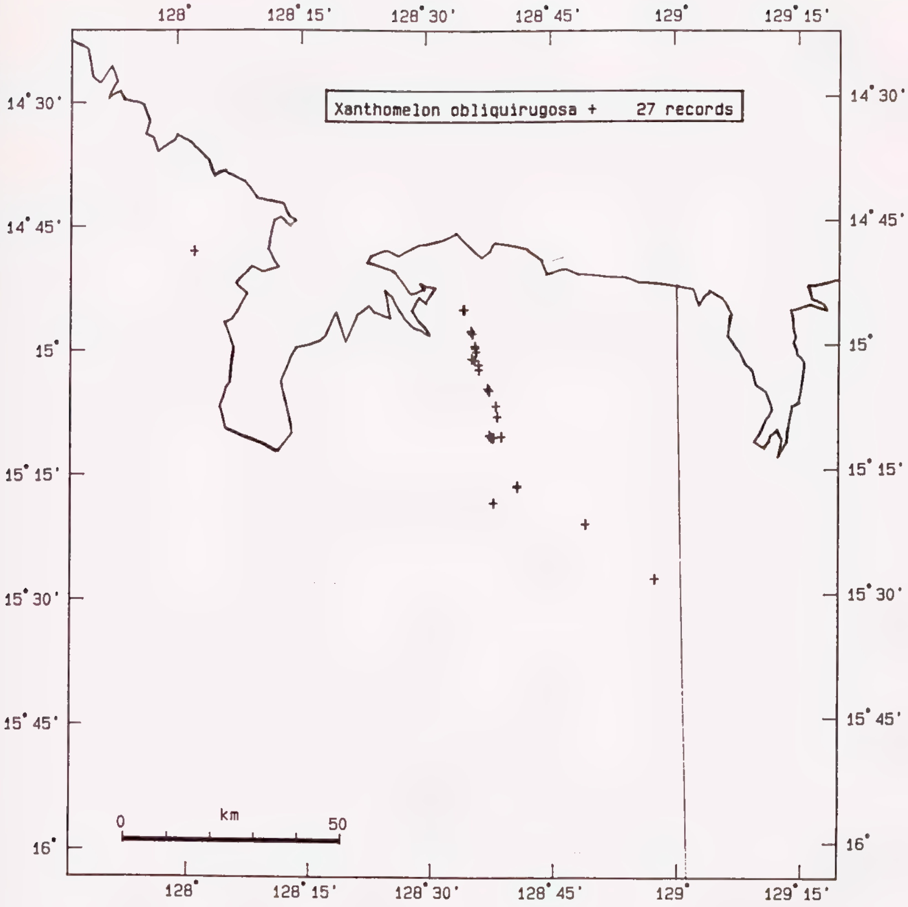
4. Distribution records of the wide ranging Kimberley species *Westracystis lissus* (E. A. Smith, 1894).



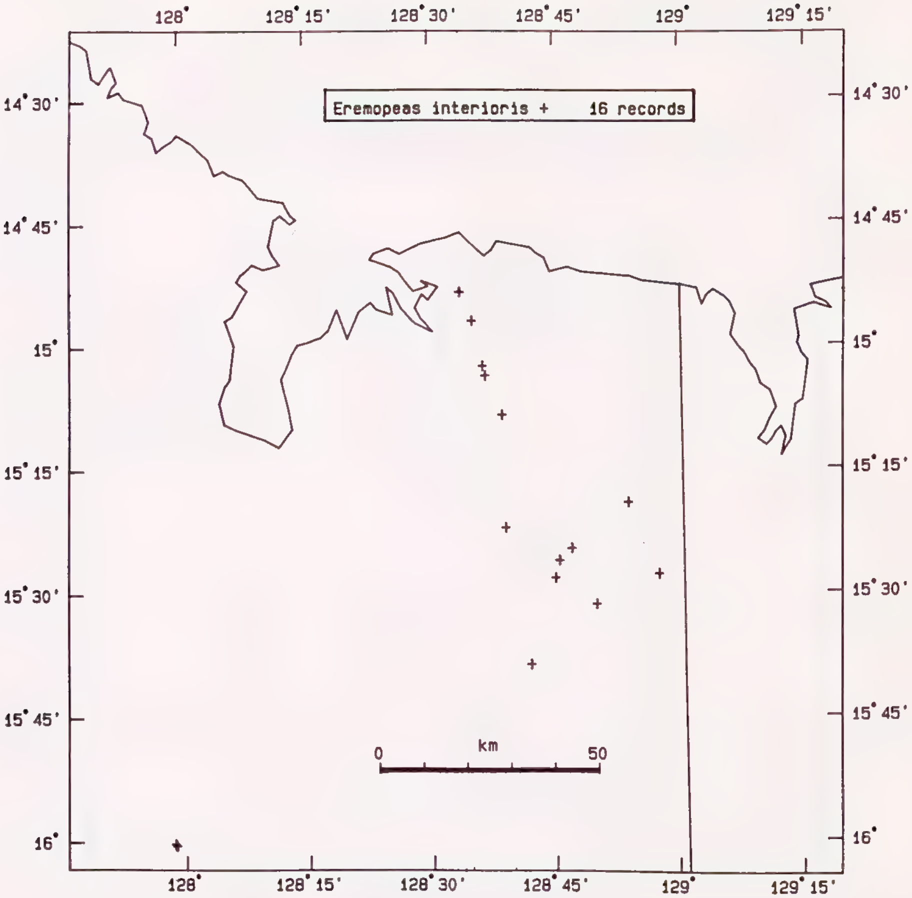
5. Distribution records of the Indonesian-New Guinea-Solomon Islands-north Australian and Red Centre species *Stenopylis coarctata* (Moellendorff, 1894).



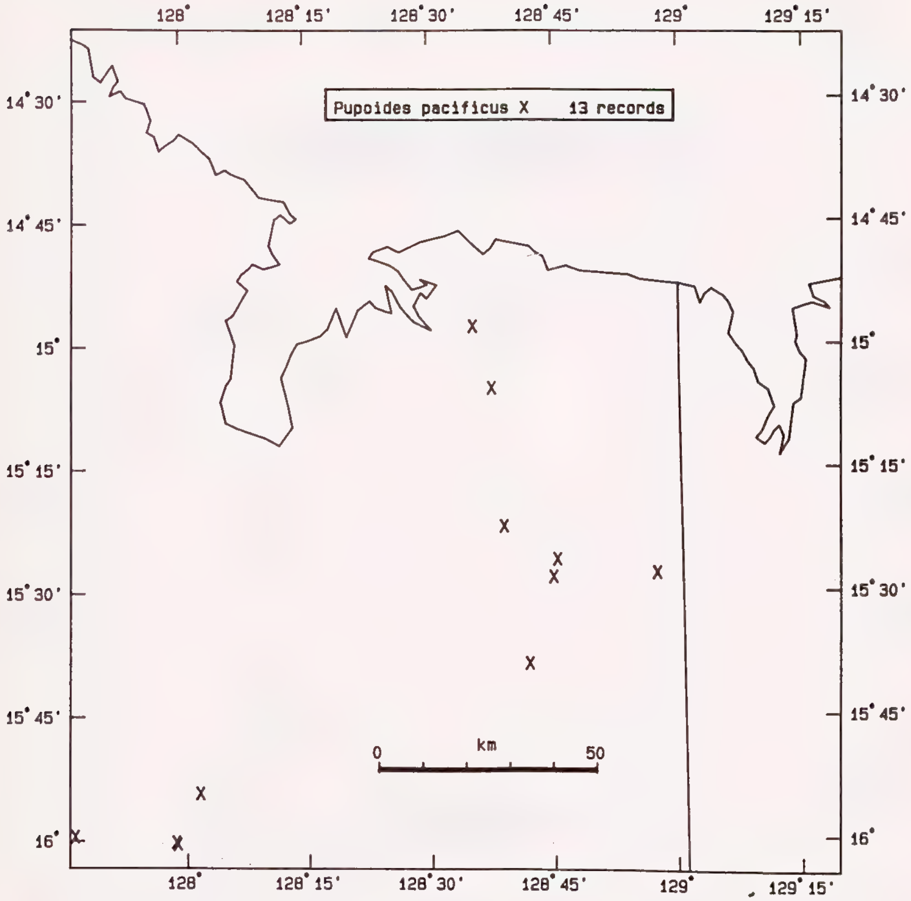
6. Distribution records of the Kimberley-Northern Territory species *Gastrocopta* new species; and Red Centre species *G. deserti* Pilsbry, 1917.



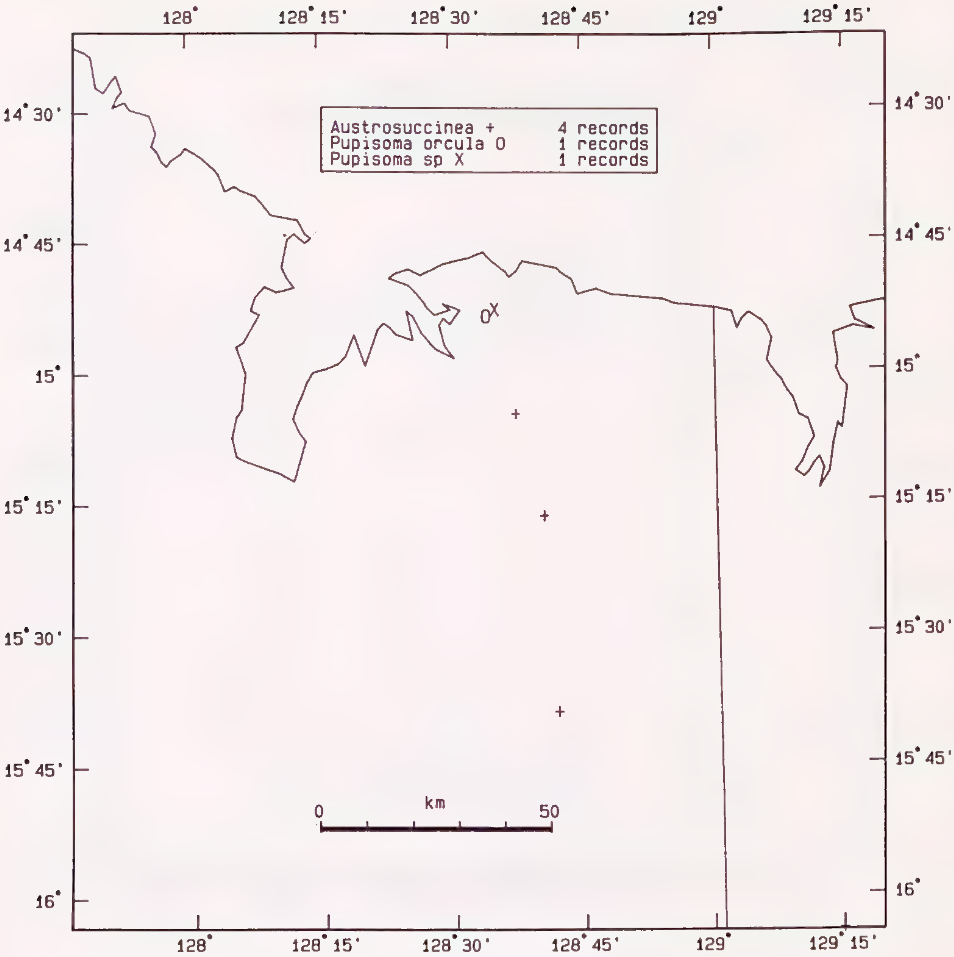
7. Distribution records of the wide ranging North Kimberley species *Xanthomelon obliquirugosa* (E. A. Smith, 1894).



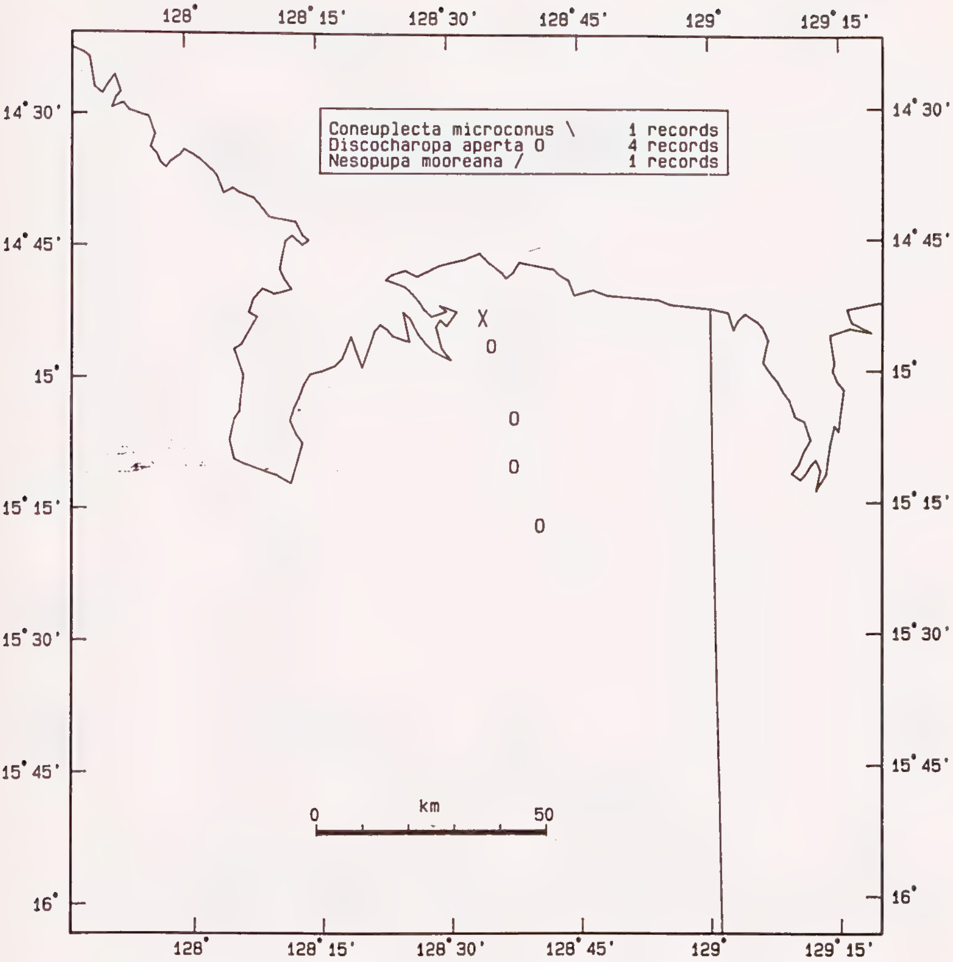
8. Distribution records of the wide ranging Kimberley and Red Centre species *Eremopeas interioris* (Tate, 1894).



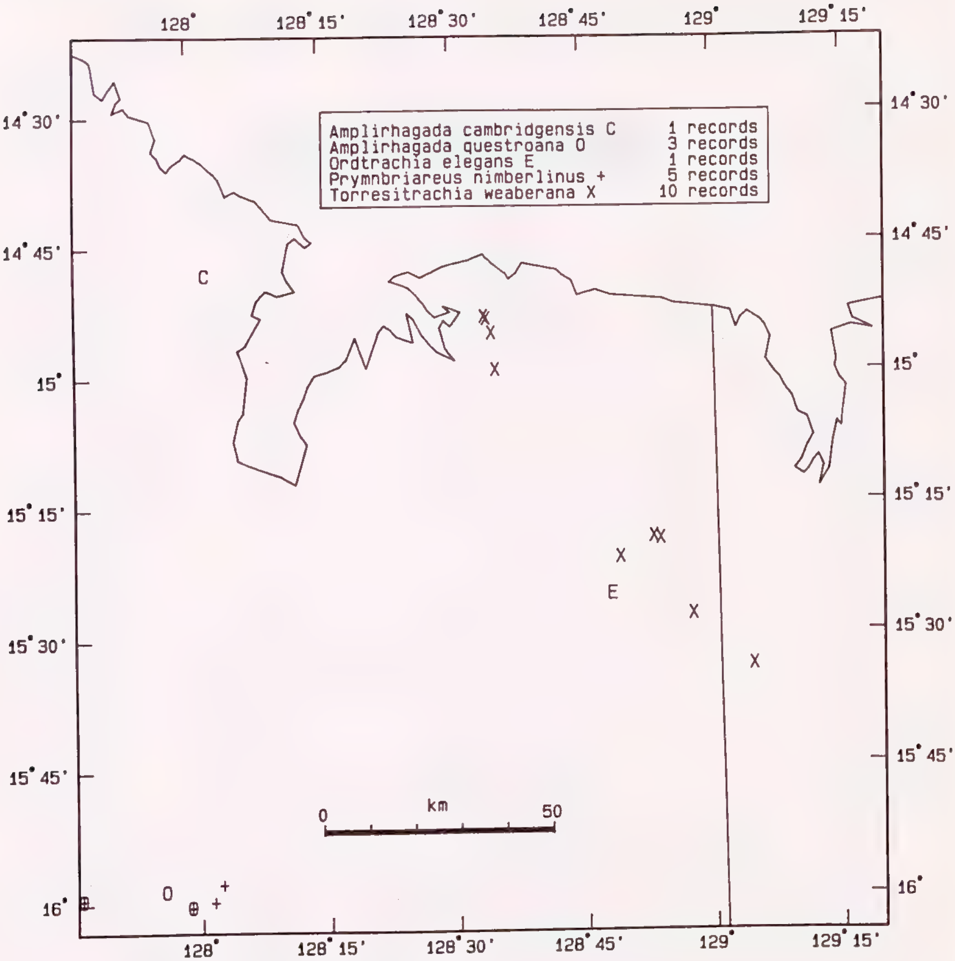
9. Distribution records of the wide ranging north Australian to New South Wales species *Pupoides pacificus* (Pfeiffer, 1846).



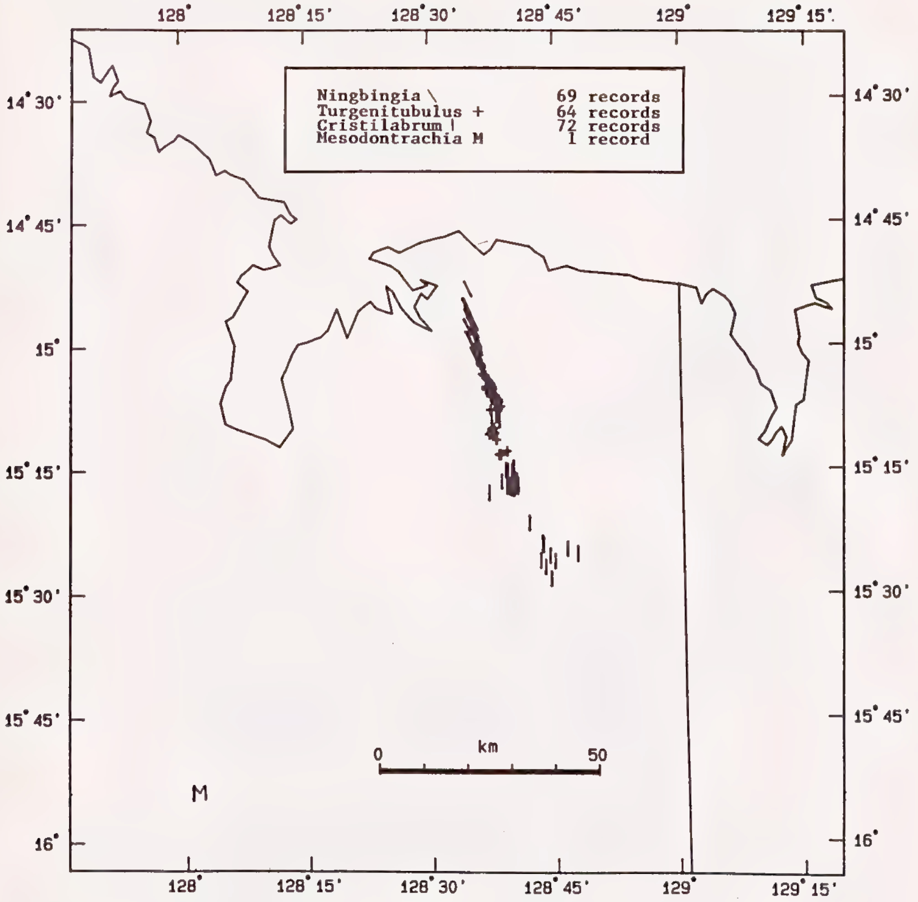
10. Distribution records of *Austrosuccinea* species; the Northern Territory and wet areas of the Kimberley species *Pupisoma orcula* (Benson, 1850) and *Pupisoma* species.


128°
128° 15'
128° 30'
128° 45'
129°
129° 15'
14° 30'
14° 45'
15°
15° 15'
15° 30'
15° 45'
16°
Coneuplecta microconus \ 1 records
Discocharopa aperta 0 4 records
Nesopupa mooreana / 1 records
X
0
0
0
0
0
km
50

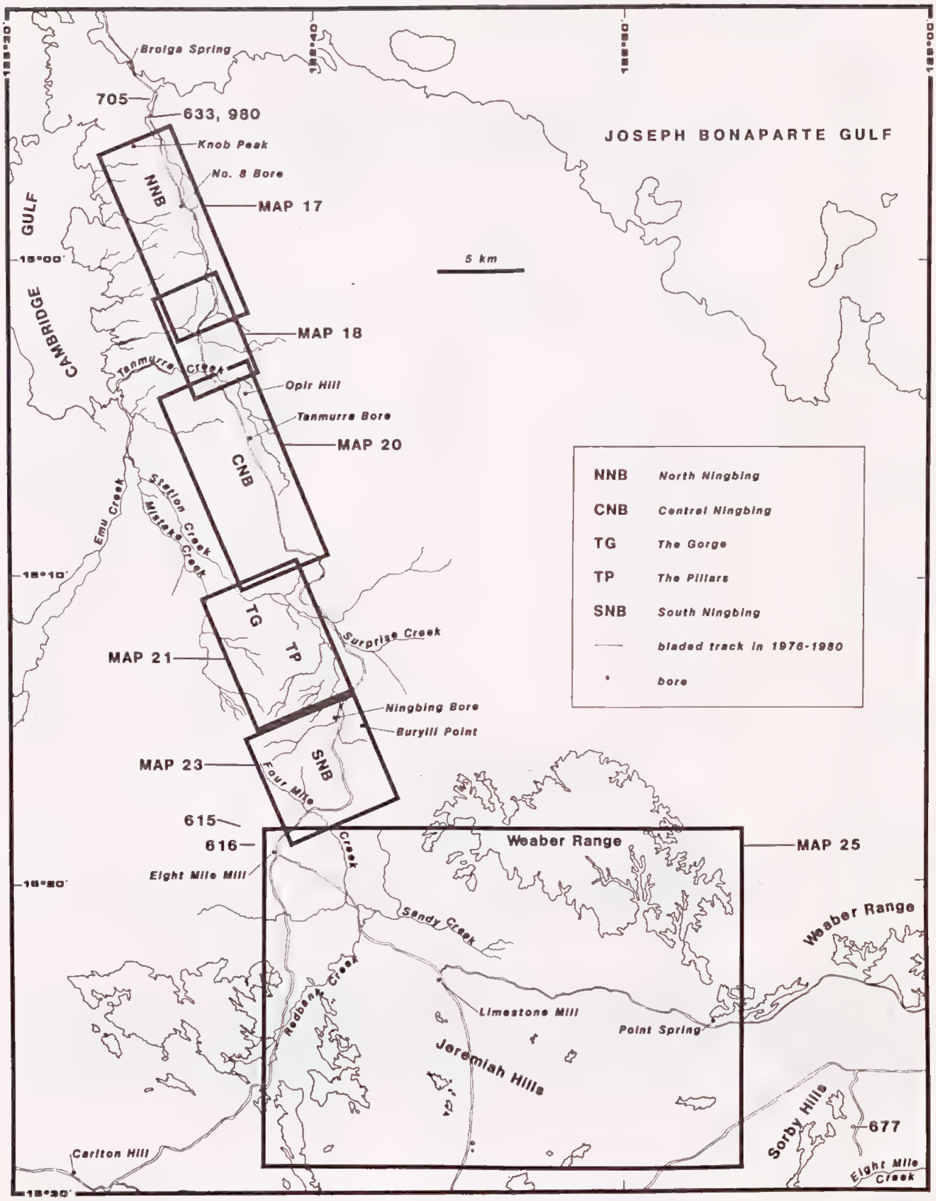
11. Distribution records of the Malaya to Samoa species *Coneuplecta microconus* (Mousson, 1865); the Phillipine to Society Islands *Discocharopa aperta* (Moellendorff, 1888); and the Roebuck Bay to Gulf of Carpenteria species *Nesopupa mooreana* (E. A. Smith, 1894).


128°
128° 15'
128° 30'
128° 45'
129°
129° 15'
14° 30'
14° 45'
15°
15° 15'
15° 30'
15° 45'
16°
Amplirhagada cambridgensis C 1 records
Amplirhagada questroana O 3 records
Ordtrachia elegans E 1 records
Prymnbriareus nimberlinus + 5 records
Torresitrachia weaberana X 10 records
C
X
E
O
+
0
km
50

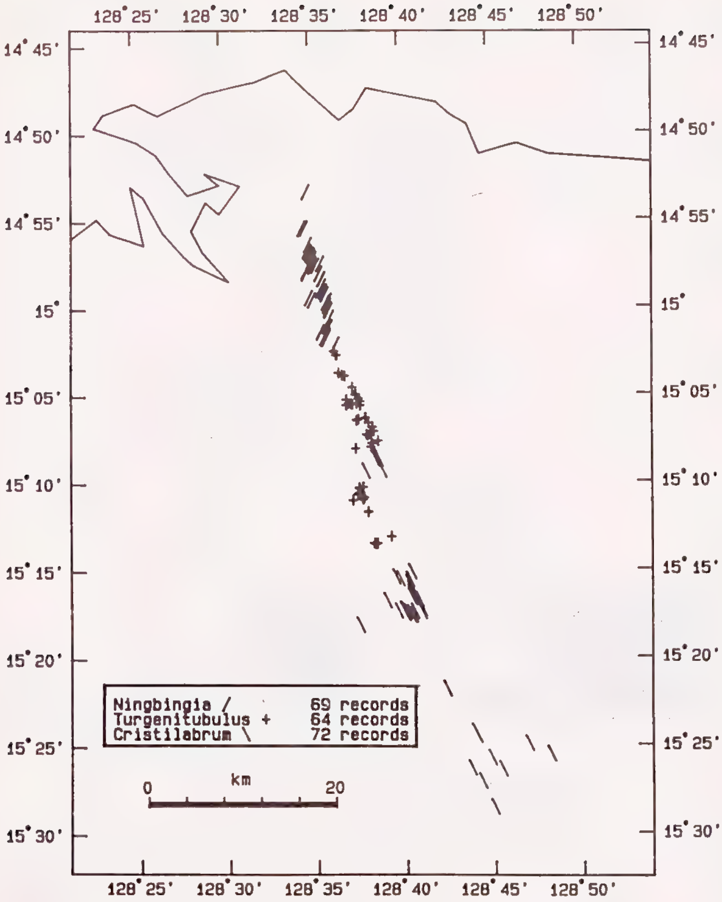
12. Distribution records of the endemic fringing taxa: *Amplirhagada cambridgensis* Solem, 1988; *Amplirhagada questroana* Solem, 1981; *Ordtrachia elegans* Solem, 1988; *Prymnbriareus nimberlinus* Solem, 1981; and *Torresitrachia weaberana* Solem, 1979.



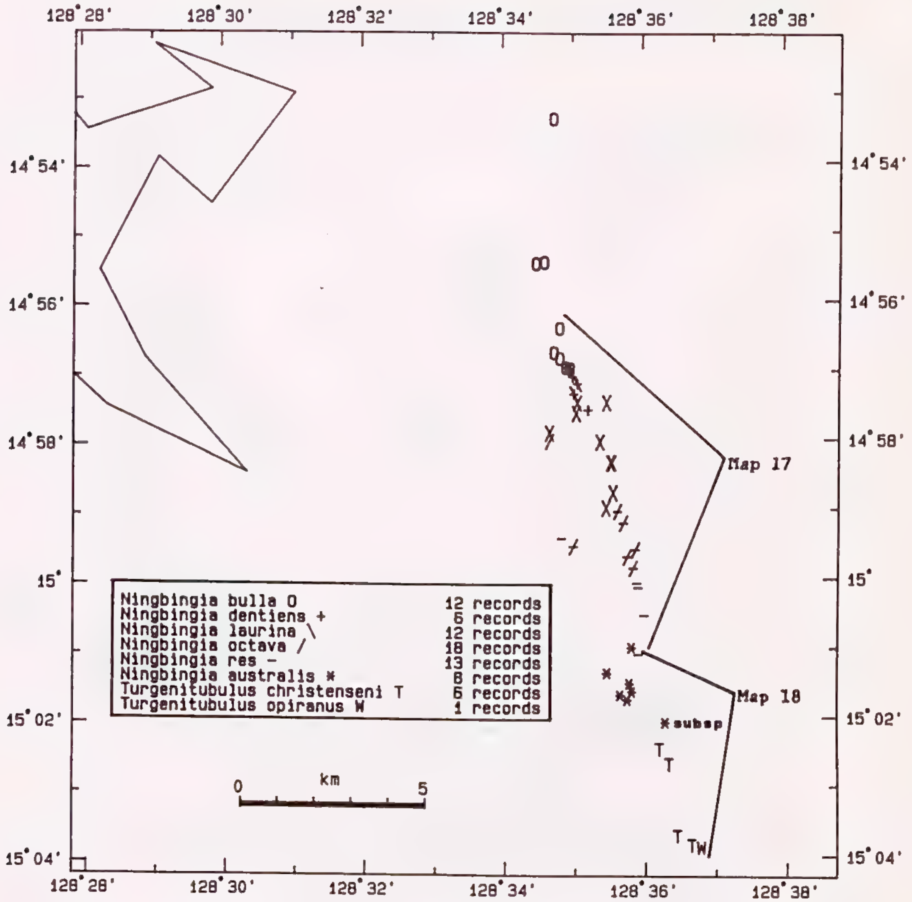
13. Distribution records of the restricted endemic taxa *Ningbingia* Solem, 1981; *Turgenitubulus* Solem, 1981; *Cristilabrum* Solem, 1981; and *Mesodontrachia cockburnensis* Solem, 1988.



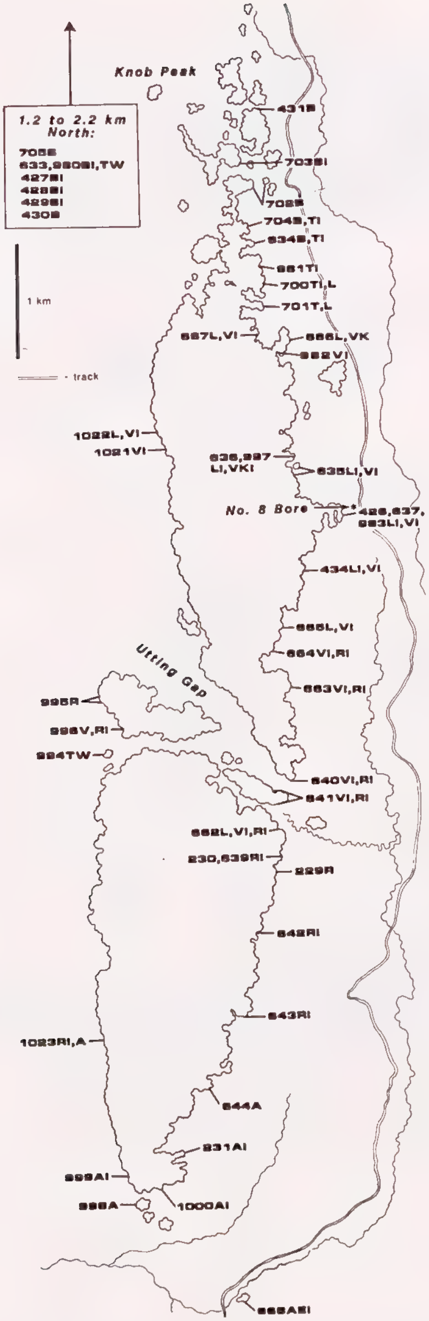
14. Ningbing Ranges and Jeremiah Hills, outlining areas covered by detailed maps of limestone exposures.



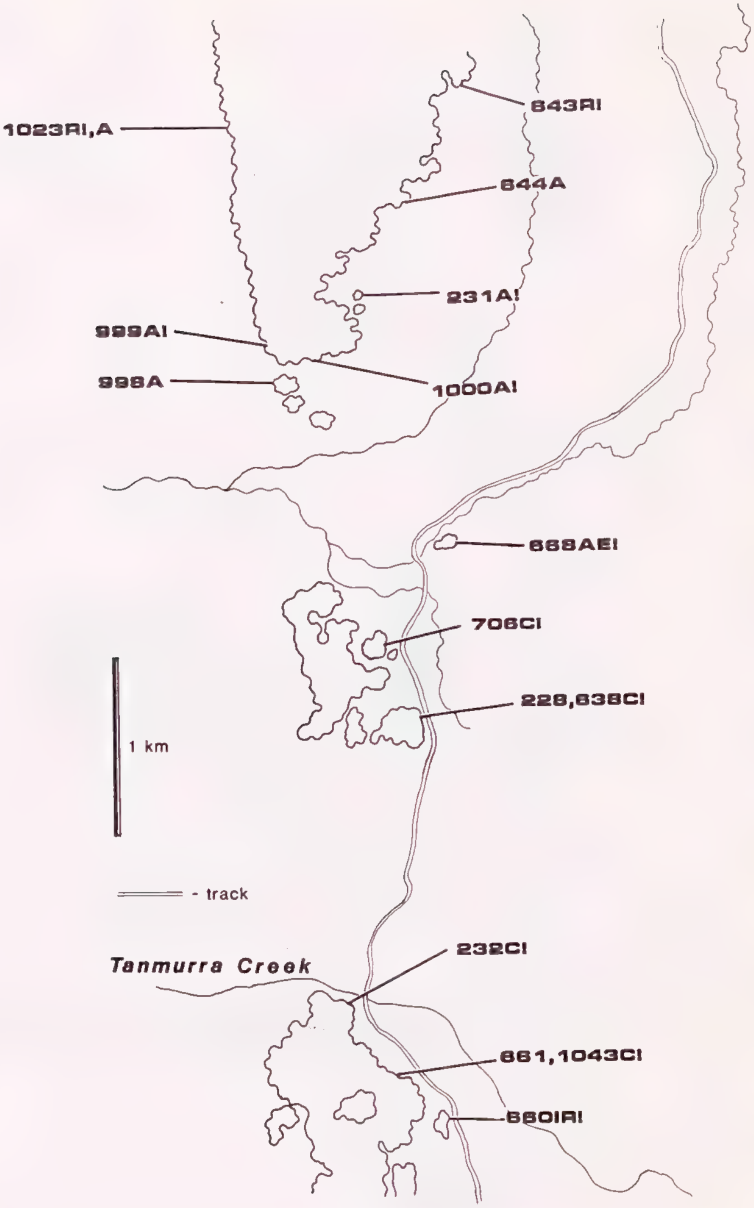
15. Ningbing Ranges and Jeremiah Hills, showing allopatric ranges of the restricted endemic genera *Ningbingia; Turgenitubulus;* and *Cristilabrum.*


128° 28'
128° 30'
128° 32'
128° 34'
128° 36'
128° 38'
14° 54'
14° 56'
14° 58'
15°
15° 02'
15° 04'
Map 17
Map 18
subsp
Ningbingia bulla O 12 records
Ningbingia dentiens + 5 records
Ningbingia laurina \ 12 records
Ningbingia octava / 18 records
Ningbingia res − 13 records
Ningbingia australis * 8 records
Turgenitubulus christenseni T 5 records
Turgenitubulus opiranus W 1 records
0
km
5

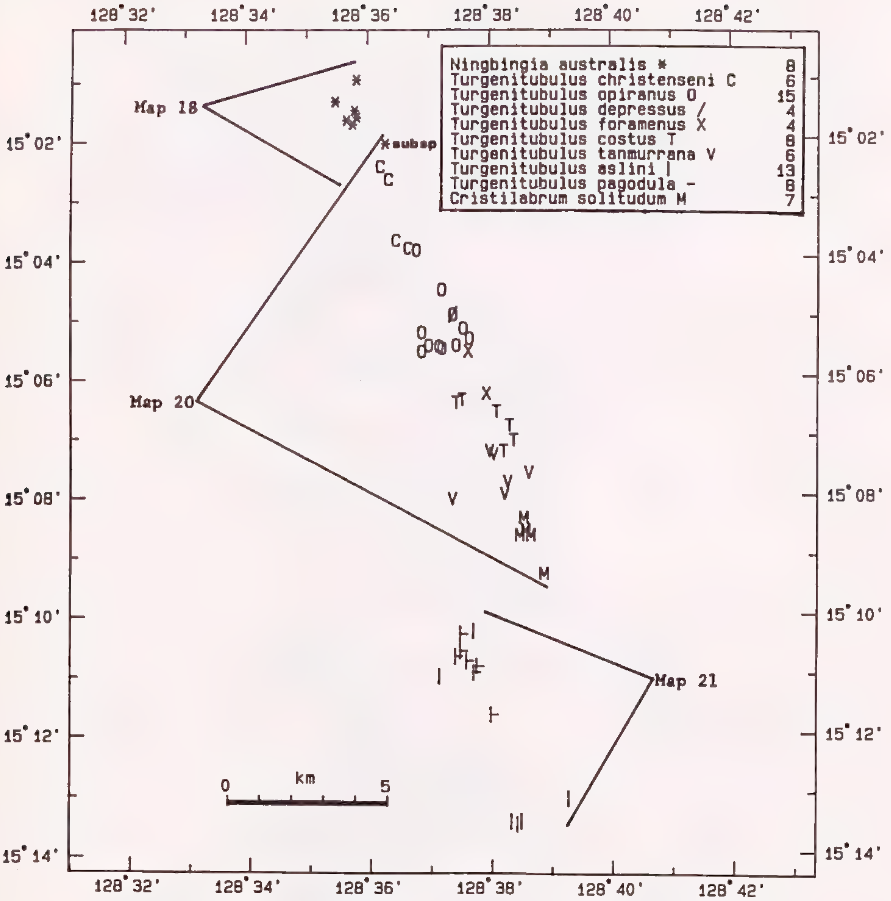
16. Distribution of *Ningbingia* species in the North Ningbing Range. The subspecies referred to is *Ningbingia australis elongata* Solem, 1988.



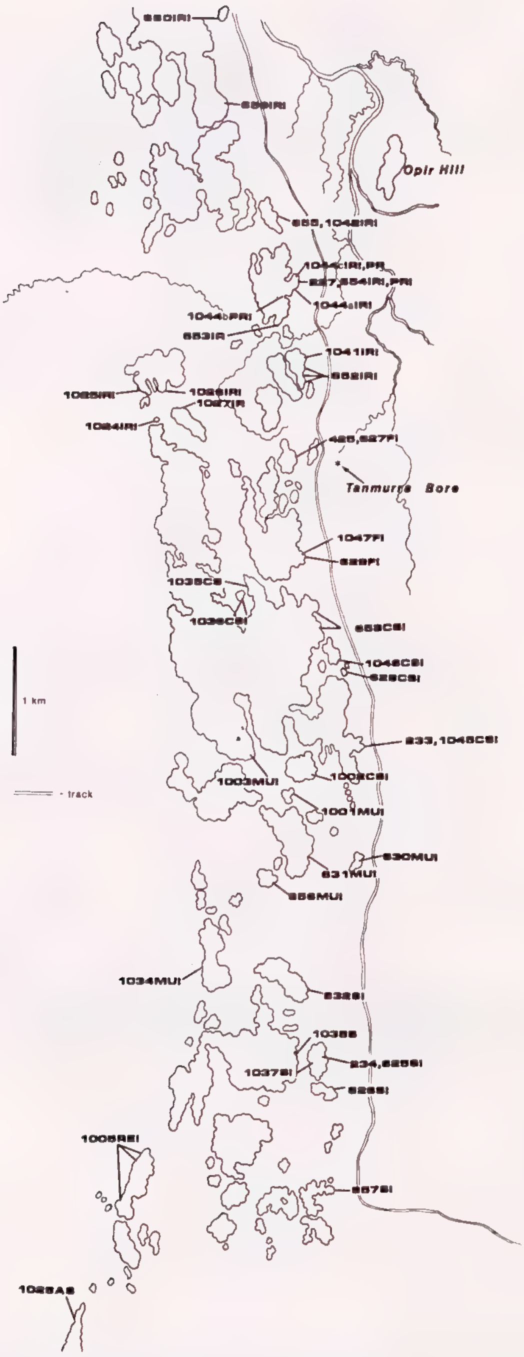
17. Species records of *Ningbingia* on the limestone masses in the North Ningbing Range. The species abbreviations are: A — *N. australis australis*; AE — *N. australis elongata*; B — *N. bulla*; L — *N. laurina*; R — *N. res*; T — *N. dentiens*; V — *N. octava* without lip knob; VK — *N. octava* with lip knob present. An "!" indicates that live adult examples were collected.



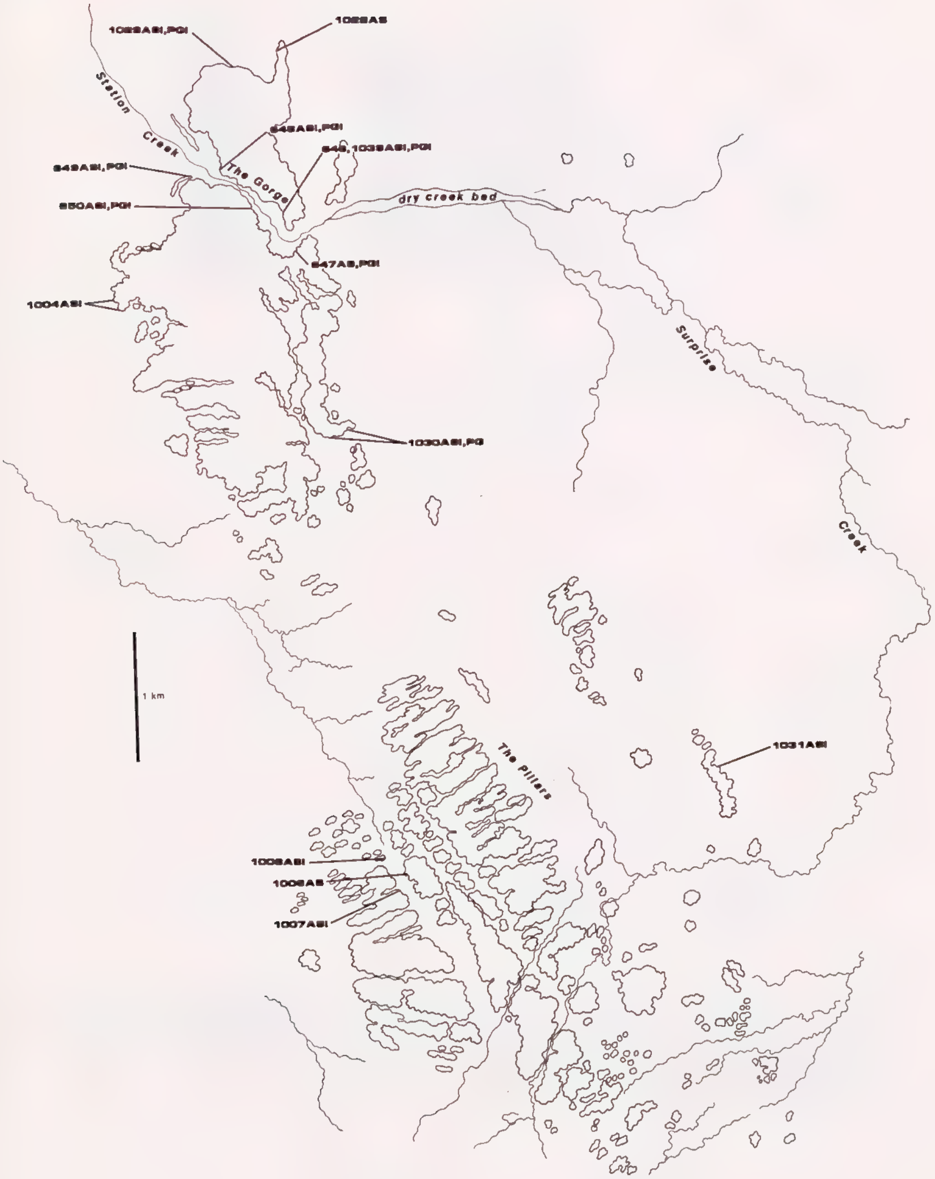
18. Species records of *Ningbingia* and *Turgenitubulus* on the limestone masses in the transition zone between the North and Central Ningbing Ranges. The species abbreviations are: A — *Ningbingia australis australis;* AE — *N. australis elongata;* R — *N. res;* C — *Turgenitubulus christenseni;* IR — *T. opiranus.* An "!" indicates that live adult examples were collected.


128° 32'
128° 34'
128° 36'
128° 38'
128° 40'
128° 42'
15° 02'
15° 04'
15° 06'
15° 08'
15° 10'
15° 12'
15° 14'
Ningbingia australis * 8
Turgenitubulus christenseni C 6
Turgenitubulus opiranus O 15
Turgenitubulus depressus / 4
Turgenitubulus foramenus X 4
Turgenitubulus costus T 8
Turgenitubulus tanmurrana V 6
Turgenitubulus aslini | 13
Turgenitubulus pagodula - 8
Cristilabrum solitudum M 7
Map 18
Map 20
Map 21
*subsp
0
km
5

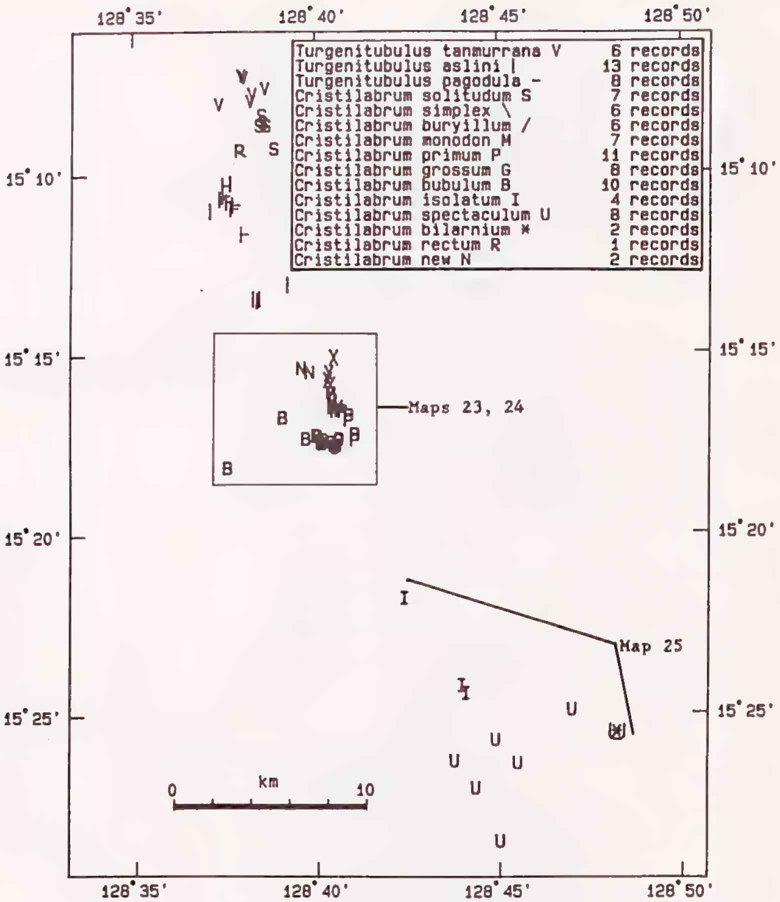
19. Distribution of *Turgenitubulus* species and *Cristilabrum solitudum* in the Central Ningbing Range, The Gorge, and The Pillars. *Cristilabrum rectum,* occurring just W of the range shown for *C. solitudum* is omitted here, but is shown on Maps 18 and 20.



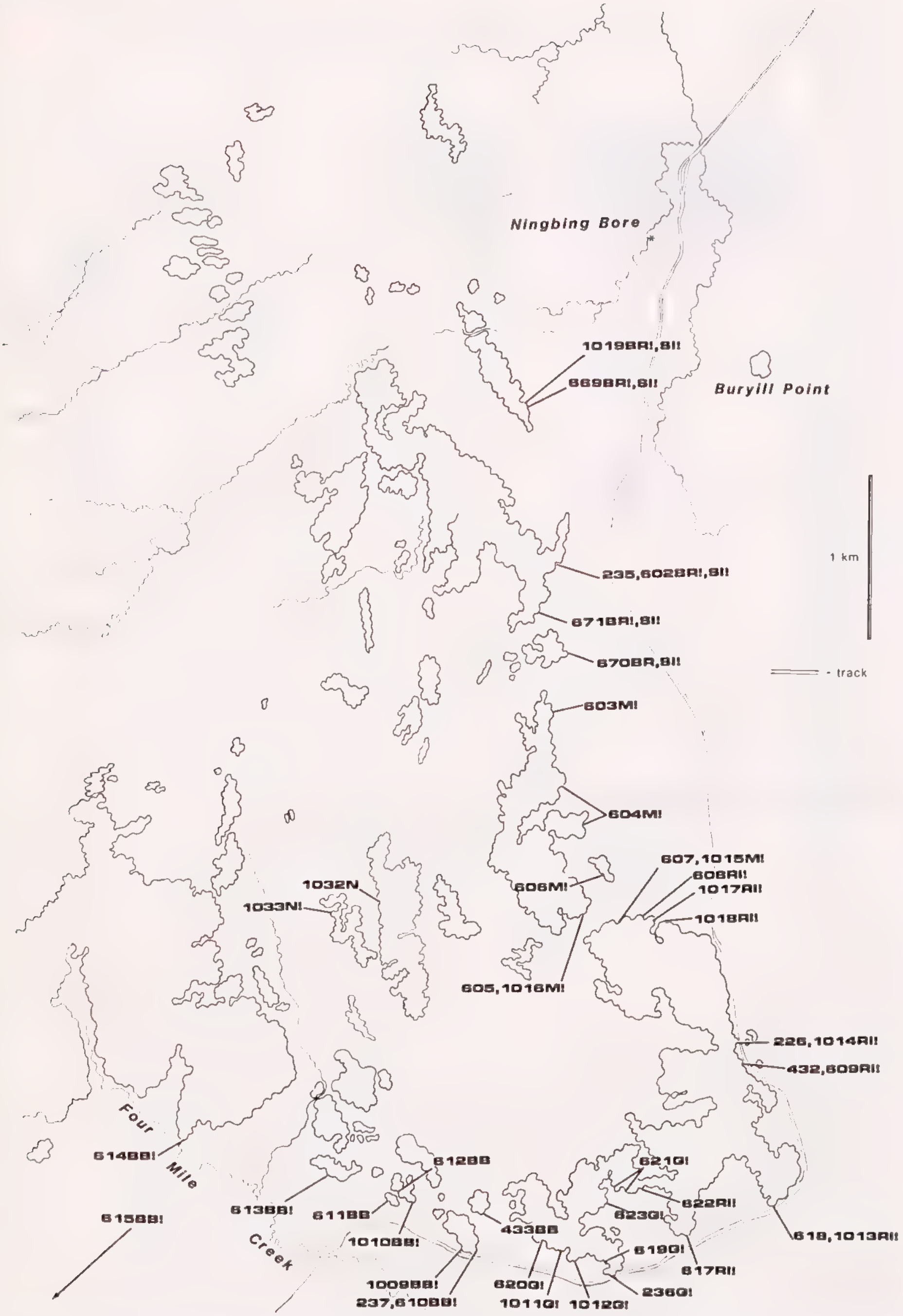
20. Species records of *Turgenitubulus* and *Cristilabrum* on limestone masses of the Central Ningbing Range. The species abbreviations are: AS — *Turgenitubulus aslini*; CS — *T. costus*; F — *T. foramenus*; IR — *T. opiranus*; MU — *T. tanmurrana*; PG — *T. pagodula*; RE — *Cristilabrum rectum*; S — *C. solitudum*. An "!" indicates that live adult examples were collected.



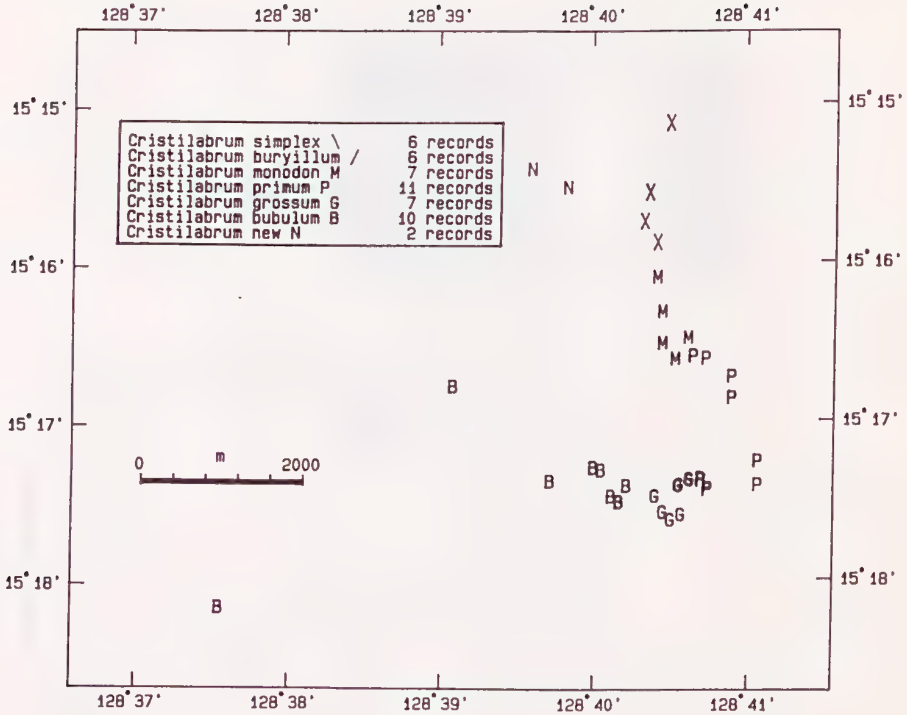
21. Species records of *Turgenitubulus aslini* (AS) and *T. pagodula* (PG) on limestone masses of The Gorge and The Pillars.


128° 35'
128° 40'
128° 45'
128° 50'
15° 10'
15° 15'
15° 20'
15° 25'
Turgenitubulus tanmurrana V 6 records
Turgenitubulus aslini | 13 records
Turgenitubulus pagodula - 8 records
Cristilabrum solitudum S 7 records
Cristilabrum simplex \ 6 records
Cristilabrum buryillum / 6 records
Cristilabrum monodon M 7 records
Cristilabrum primum P 11 records
Cristilabrum grossum G 8 records
Cristilabrum bubulum B 10 records
Cristilabrum isolatum I 4 records
Cristilabrum spectaculum U 8 records
Cristilabrum bilarnium * 2 records
Cristilabrum rectum R 1 records
Cristilabrum new N 2 records
Maps 23, 24
Map 25
0
km
10

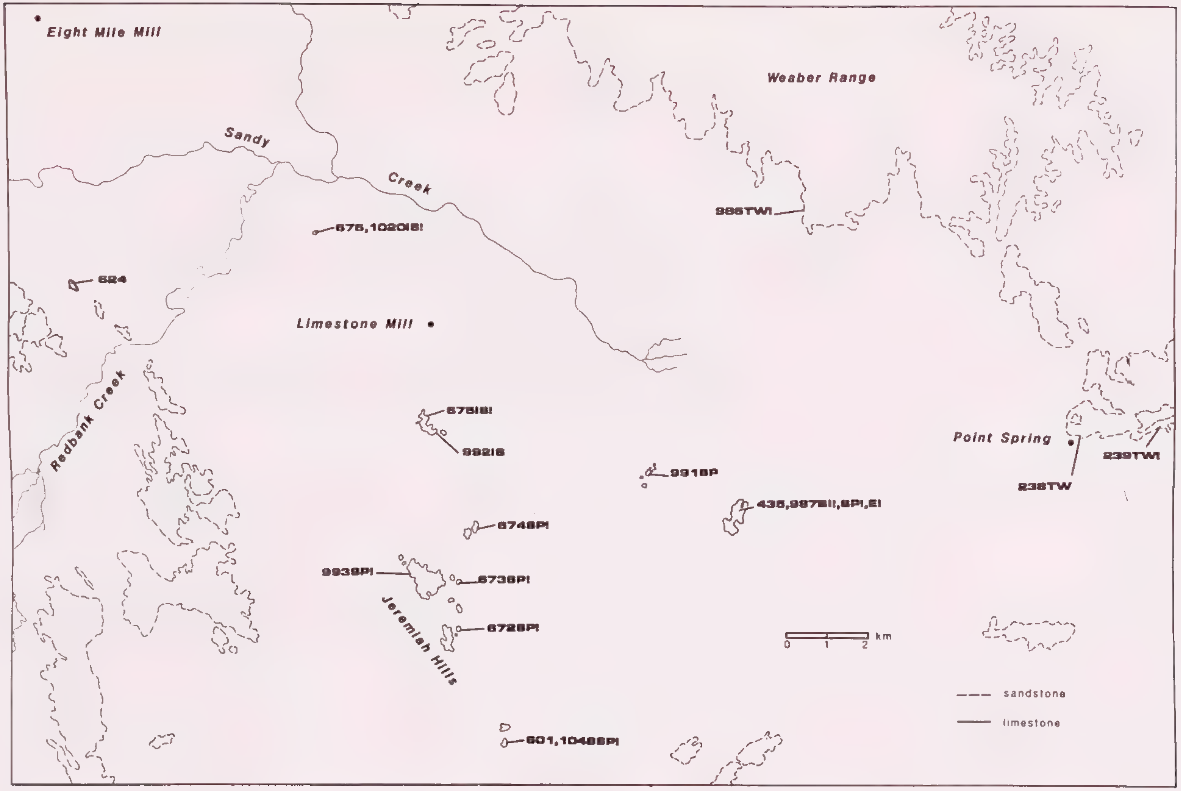
22. Distribution of *Turgenitubulus* and *Cristilabrum* species in the area from the south tip of the Central Ningbing Range, The Gorge, The Pillars, South Ningbing Range, and Jeremiah Hills. The single record for *Cristilabrum bilarnium* (*) in the SE corner of the map, also is the only known locality for *Ordtrachia elegans* (see Map 10).



23. Species records of *Cristilabrum* on limestone masses of the South Ningbing Range. The species abbreviations are: BB — *Cristilabrum bubulum*; BR — *C. buryillum*; G — *C. grossum*; M — *C. monodon*; N — *C.* probably new species; RI — *C. primum*; SI — *C. simplex*. An "!" indicates live adult examples were collected.


128° 37'
128° 38'
128° 39'
128° 40'
128° 41'
15° 15'
15° 16'
15° 17'
15° 18'
Cristilabrum simplex \ 6 records
Cristilabrum buryillum / 6 records
Cristilabrum monodon M 7 records
Cristilabrum primum P 11 records
Cristilabrum grossum G 7 records
Cristilabrum bubulum B 10 records
Cristilabrum new N 2 records
0 m 2000

24. Distribution of *Cristilabrum* species in the South Ningbing Range.



25. Distribution of *Cristilabrum* species; *Ordtrachia elegans* Solem, 1988; and *Torresitrachia weaberana* Solem, 1979 in the Jeremiah Hills and Weaber Ranges. Station WA-624, at the left of the map, was on a small limestone hill from which no camaenids were collected. The species abbreviations are: BI — *Cristilabrum bilarnium*; IS — *C. isolatum*; SP — *C. spectaculum*; E — *Ordtrachia elegans*; TW — *Torresitrachia weaberana*. An "!" indicates that live adult examples were collected.